Information Gathering Prior to Emigration in House-Hunting Ants

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ABSTRACT

In large animal groups, collective decision-making is often self-organised, i.e. decisions emerge from local interactions between individuals following simple behavioural rules. It is often assumed that no great cognitive complexity or diversity is required in individuals to produce complex, finely tuned collective choices. In this thesis, I investigate whether collective decisions can benefit from individual memories and previous experience in house-hunting by the rock ant *Temnothorax albipennis*. Rock ants emigrate readily into a new home if their current nest is damaged. During emigrations, colonies can select the best available site using distributed decision-making mechanisms. Here, I show that rock ants continually gather information about available nest sites, even when their home nest is still intact. This leads to a generally improved collective performance in later emigrations. Prior familiarisation with high-quality nest sites indeed allows colonies to emigrate faster, be more cohesive and/or choose more accurately than naïve colonies, thus leading to a better compromise between speed and accuracy. Additionally, rock ants appear to adjust their preference criteria according to the respective qualities of their home nest and of available nest sites. This confers colonies with high flexibility in their choices and allows them to tune collective decisions according to external conditions. I also provide evidence that workers memorise the position and suitability of high-quality, available nest sites. They then retrieve that memory, to play a key role in later emigrations. Additionally, nest marking chemicals and social interactions within previously visited, candidate nest sites ensure effective transfer of information to naïve workers during emigrations. These results indicate that ants have high individual cognitive abilities, as they can memorise information and retrieve it later, and that certain individuals are disproportionately influential in subsequent collective choices. This suggests that distributed decision-making may greatly benefit from both individual cognitive complexity and inter-individual variability.

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AUTHOR'S DECLARATION

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated below, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

All work presented in Chapter II, Chapter IV and Chapter V, Section A and Section B is entirely the candidate's own work. The model presented in Chapter III and in the Appendix was written by James A. R. Marshall and Patrick M. Hogan following discussions with the candidate. The experimental data presented in Chapter III and Chapter V, Section C was collected by visiting students, but the analysis, graphs and interpretations of this data are entirely the candidate's own work.

SIGNED: ..... DATE:.....

NOTE ON THESIS STYLE

All of the chapters in this thesis are written in the style of scientific papers. I was encouraged to use this approach to speed the publication of this work. As a consequence, in data chapters, 'we' is used instead of 'I', because these chapters have been or will be submitted to journals with my advisors as co-authors. However, to facilitate reading, I have removed overlapping and redundant sections whenever possible, and I have homogenised the format of chapters throughout the thesis.

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GENERAL INTRODUCTION

Chapter I. General Introduction

Random groups of individuals can be surprisingly apt at solving complex, cognitively demanding tasks or at predicting the outcome of uncertain future events. Human groups can sometimes collectively outperform even smart individuals (Krause *et al.* 2010; Surowiecki 2004). This is known as 'the wisdom of crowds' and has been widely studied by sociologists and psychologists endeavouring to optimise decision-making by teams and committees in large companies (Austen-Smith & Feddersen 2009; Kerr & Tindale 2004). Examples of how humans exploit collective intelligence are plentiful in daily life (Krause *et al.* 2010; Surowiecki 2004), ranging from the algorithms underlying common search engines such as Google (Page *et al.* 1999) to the forecasting of election results based on prediction markets (Leigh & Wolfers 2006; Wolfers & Zitzewitz 2004) and the collective management of sport teams (Krause *et al.* 2010). The ability of large groups to access high-order cognitive capacities has been known for a long time. In 1907, for example, the British scientist Galton observed that the collective estimate of an ox's weight (averaged over 800 participants in a weight-judging competition) was very accurate, differing from the actual weight by less than 1%, and outperforming the best individual guess (Galton 1907). This principle was formalised, in the 18th century, by a French intellectual Nicolas de Condorcet: in his Jury Theorem, Condorcet showed that majority decisions by groups of individuals making independent judgments are more likely to be correct than individual decisions, and that collective accuracy increases with group size (Boland 1989; King & Cowlishaw 2007; List 2004). Group decisions are expected to be more accurate than individual decisions provided group members have diverse sources of information and independently evaluate the alternatives before opinions are collated to produce a common decision. This ensures that a large array of solutions is explored and minimises the risk of amplifying individual biases (Austen-Smith & Feddersen 2009; Kerr & Tindale 2004; Krause *et al.* 2010; Surowiecki 2004).

The application of self-organisation principles (i.e. emergence of complex collective patterns from local interactions between sub-units) to the study of large animal groups (Bonabeau *et al.* 1997; Camazine *et al.* 2001; Deneubourg & Goss 1989) recently opened the door to new investigations of the collective intelligence of non-human groups. Self-organisation indeed provided a new theoretical framework that led to the identification of mechanisms – such as positive feedback and quorum sensing – allowing efficient transfer of information, opinion polling and consensus achievement based on simple rules of thumb in

vertebrates and invertebrates (Couzin & Krause 2003; Couzin *et al.* 2005; Franks *et al.* 2002; Marshall *et al.* 2009; Sumpter 2006; Sumpter & Pratt 2009; Visscher 2007). Accordingly, a rising number of studies have shown that animal groups can solve highly complex tasks and achieve high-order cognitive and computational capacities that go beyond that of individuals (Couzin 2007; Couzin 2009), as well as make decisions collectively (Conradt & Roper 2005).

Collective decision-making in human and animal groups share many similarities and raise comparable questions. Recent work (reviewed in Conradt & List 2009) has therefore attempted to compare and reconcile approaches to the study of group decisions in the social and the natural sciences. In particular, three central factors appear to have a major influence on the accuracy of collective decisions: (i) sharing of information among individuals; (ii) presence or absence of conflicts of interests among group members; and (iii) existence of side constraints such as time limits. Conflicts of interests are of particular relevance because they influence the mechanisms by which a consensus is reached. In animal groups, when individuals vary in their preferred decision outcome, natural selection is expected to favour mechanisms which optimise the balance between the costs incurred by sub-optimal decisions and the benefits of maintaining group cohesion (Conradt *et al.* 2009; Conradt & List 2009; Conradt & Roper 2009). In humans, conflicts of interests between individuals may however lead to more complex situations. Decision committees might explicitly aim at maximising the overall pay-offs across the group (Conradt & List 2009). However, in many cases conflicts of interests can induce individuals to conceal or report untruthfully their private information (Austen-Smith & Feddersen 2009), to attempt to influence other group members (Wood 2000) or to form alliances (Conradt & List 2009), so as to increase the likelihood of their preferred outcome being chosen. In such conditions collective decisions might not lead to the group optimum – in extreme cases this might even result in failure to reach consensus (Conradt & List 2009). By contrast, situations in which all group members share the same interests (Conradt & Roper 2005) or, in humans, the same objectives and/or values (Austen-Smith & Feddersen 2009) favour decision mechanisms that lead to optimal, accurate collective choices. This is particularly relevant in collective decision-making by social insect colonies (ants, bees, wasps and termites; Conradt & Roper 2005), where a high relatedness among individuals tends to favour cooperation and limit conflicts of interests (mostly restricted to reproductive division of labour; see e.g. Bourke & Franks 1995).

Studying the mechanisms underlying biological systems may provide useful insights for optimality in problem solving and decision-making (Marshall *et al.* 2009), because natural selection is expected to have shaped rules of thumbs that perform well in most natural conditions (Houston *et al.* 2007). This may in turn provide new solutions for problem solving and decision-making in engineering. In particular, the study of self-organisation and collective

decision-making by social insects has raised a lot of interest beyond biology. This is partly because insects are usually considered as relatively simple units, so their behaviour can be easily modelled (Pratt *et al.* 2005) or reproduced (Beni 1989). Additionally, colonies of social insects are confronted with difficulties and constraints that are common in artificial systems (Marshall *et al.* 2006), such as the necessity to find a good compromise between the speed and accuracy of decisions. Improving one of these two dimensions indeed usually results in a decrease in performance in the other dimension, both in biology (Chittka *et al.* 2009; Franks *et al.* 2009; Franks *et al.* 2003a; Marshall *et al.* 2009; Marshall *et al.* 2006; Passino & Seeley 2006; Sumpter & Pratt 2009) and engineering (Djamarus & Ku-Mahamud 2008; Marshall *et al.* 2006). Social insects have therefore inspired diverse applications in engineering domains. For example, the concept of Swarm Intelligence (a term derived from swarms of honeybees and generally referring to the high cognitive abilities of both human and animal groups; see Bonabeau *et al.* 1999b; Krause *et al.* 2010) was successfully applied to robotics (Swarm Robotics; see Beni 1989; Beni 2005). Additionally, some problem solving artificial algorithms (e.g. Ant Algorithm and Ant Colony Optimisation) were inspired from mechanisms of collective foraging in ants (Djamarus & Ku-Mahamud 2008; Ratnieks 2008).

The concepts of self-organisation and swarm intelligence have greatly contributed to the understanding of collective processes in large animal groups (Bonabeau *et al.* 1997; Camazine *et al.* 2001; Couzin 2007; Couzin 2009; Couzin & Krause 2003). However, the classical juxtaposition of 'individual simplicity vs. collective complexity', suggested in early studies on self-organisation in social insects (Deneubourg 1995), is an oversimplification. There is accumulating evidence that individuals are themselves complex integrators of information (Seeley 2010a; Seeley 2010b). Key individuals can play a major role in self-organised processes and be disproportionately influential on collective decisions. This has been particularly well studied in synchronised movements by large vertebrate groups, where effective leaders arise if they have access to pertinent information (Couzin *et al.* 2005; Dyer *et al.* 2009; Faria *et al.* 2010a; Lusseau & Conradt 2009) or if their interest diverges from the rest of the group (Conradt *et al.* 2009). In social insects, there is also evidence that some key individuals (either well-informed or behaviourally specialised) are particularly important in the organisation of division of labour (Anderson & Ratnieks 1999; Fewell 2003; Gordon 2002; Jackson *et al.* 2006; O'Donnell & Bulova 2007; Robson & Traniello 1999; Sendova-Franks *et al.* 2010). One could expect individuals that possess pertinent information to have a strong influence on collective decision making in social insects, as it is the case in vertebrates. Indeed, natural selection can be expected to have favoured mechanisms that allow the entire group to benefit from valuable information gathered independently by individuals, since, as mentioned above, conflicts of interests are limited in these highly cooperative societies. Nest site selection by house-hunting social insects provides one such example. During

emigrations (ants) or swarming (honeybees), the relocation of the entire colony is indeed organised by a minority of workers (the scouts), which explore the environment in search for suitable nesting sites (Franks *et al.* 2002; Visscher 2007). In honeybees, scouts that have discovered a suitable site come back to the swarm and advertise that site by performing the waggle dance, thereby recruiting other scouts to that site (Lindauer 1957; Seeley & Burhman 1999). This process occurs simultaneously for multiple sites discovered independently, until a consensus is reached among scouts for a single nest site (Seeley & Visscher 2003; Seeley & Visscher 2004a; Seeley & Visscher 2004b). The swarm then takes off and flies to its new home. At the time of take-off, only a minority of bees (typically less than 5%) have visited the new nest site and therefore its location. These informed scouts are however able to guide the entire swarm by flying through it at a high speed in the correct direction (Schultz *et al.* 2008). This example illustrates how a minority of informed workers can influence and organise both decision-making and decision implementation by an entire swarm of honeybees (Britton *et al.* 2002). However, whether specific scouts might have more influence on the collective decision outcome than others – e.g. by following different behavioural rules, as suggested by Conradt & List (2009) – remains to be investigated.

Another timely question concerns the potential influence of previous experience and memory on collective decision-making. Individuals are capable of learning, i.e. of modifying their behavioural responses according to previous experience (Pearce 1997). Learning abilities are widespread in animals, including invertebrates, and have been shown to be particularly well developed in some insects such as ants (Djieto-Lordon & Dejean 1999; Dupuy *et al.* 2006; Johnson 1991; Schneirla 1933) and honeybees (Giurfa 2003; Menzel & Giurfa 2006). Individual learning in the context of a collective task is likely to increase the performance of individuals and the efficiency of inter-individual interactions, therefore improving the group's collective performance in that specific task. This was indeed shown to occur in the context of successive emigrations by house-hunting ants (Langridge *et al.* 2004; Langridge *et al.* 2008a; Langridge *et al.* 2008b). Additionally, individuals can memorise information about potentially available resources, and then retrieve and use that memorised information later, when the need to exploit and/or to choose among alternative resources arises. This is usually beneficial, e.g. because gathering information early allows individuals later to invest more in other, crucial activities; or because time constraints or seasonal variations make it impractical to access the relevant information when the time to make a decision has come (e.g. learning for the future in parasitic wasps; see Collett 2008; or prospecting in birds; see Danchin *et al.* 2001). Animal groups faced with a decision could similarly be expected to benefit from the use of information about available options previously gathered by some of their group members. This aspect of collective decision-making has received little attention so far, and raises interesting questions: if groups do exploit prior

information gathered independently by individuals, then how is that information stored, and then retrieved and shared among group members during the decision-making process? Additionally, if a few well-informed individuals have a particularly strong influence on the outcome of collective choices, then the condition of independency of individual evaluation presented above is not fulfilled and this could introduce possible bias in the final decision. How do animal groups find an appropriate balance between exploiting valuable individual information and maintaining accurate, unbiased choices?

Nest site selection by emigrating colonies of house-hunting ants *Temnothorax* sp. is particularly well suited to investigate these various issues. *Temnothorax* colonies are indeed able to select the best among a large array of available new nest sites using a decentralised, self-organised decision-making process (Franks *et al.* 2002; Pratt & Sumpter 2006; Pratt *et al.* 2005; Visscher 2007). Additionally, previous studies suggested that some individuals might play a more important role on the colony's final decision than others, although this is controversial (Mallon *et al.* 2001; Robinson *et al.* 2009b). Finally, it was shown that colony performance can improve with experience over successive emigrations (Langridge *et al.* 2004) and that collective choices can be influenced by prior information about available options (Franks *et al.* 2007b) in the species *Temnothorax albipennis*. *T. albipennis* is also well-suited for the analysis of the interplay between individual and collective processes due to the small size of colonies (around 100-200 workers). This facilitates individual marking and monitoring of all workers in the colony (Mallon *et al.* 2001; Sendova-Franks & Franks 1995).

Building on a previous study by Franks *et al.* (2007b), this study investigates further how collective choices and performance are affected by prior familiarisation with one or several alternative options in emigrating colonies of *T. albipennis*; and what mechanisms are responsible for the collective exploitation of information originally gathered independently by individuals. The present thesis is therefore organised in two main parts. In the first part, I will present data on the influence of pre-emigration familiarisation with high-quality (Chapter II, p11) and low-quality (Chapter III, p31) available nest sites on collective performance. In the second part, the relative roles of key, informed individuals and of naïve individuals will first be considered during emigrations to high-quality, familiar nest sites (Chapter IV, p53). I will then present data on the type of information stored about familiar nest sites and the mechanisms underlying retrieval and transfer of that information during later emigrations (Chapter V, p69). In that chapter, I will in turn consider navigation to familiar high-quality nest sites (Section A, p69); assessment of familiar, high-quality nest sites (Section B, p83); and assessment to familiar, low-quality nest sites (Section C, p117). I will then discuss the implications of this work with regard to collective decision-making and swarm intelligence in animals, humans and artificial systems (Chapter VI, p133).

PART I – THE EFFECTS OF PRE-EMIGRATION FAMILIARISATION WITH AVAILABLE NEST SITES ON COLLECTIVE PERFORMANCE IN HOUSE-HUNTING ANTS

Chapter II. Improving Decision Speed, Accuracy and Group Cohesion through Early Information Gathering in House-Hunting Ants

ABSTRACT

Successful collective decision-making depends on groups of animals being able to make accurate choices while maintaining group cohesion. However, increasing accuracy and/or cohesion usually decreases decision speed and vice-versa. Such trade-offs are widespread in animal decision-making and result in various decision-making strategies that emphasise either speed or accuracy, depending on the context. Speed-accuracy trade-offs have been the object of many theoretical investigations, but these studies did not consider the possible effects of previous experience and/or knowledge of individuals on such trade-offs. The present study aims at investigating how previous knowledge of their environment may affect emigration speed, nest choice and colony cohesion in emigrations of the house-hunting ant *Temnothorax albipennis*, a collective decision-making process subject to a classical speed-accuracy trade-off. Colonies allowed to explore a high quality nest site for one week before they were forced to emigrate found that nest and accepted it faster than emigrating naïve colonies. This resulted in increased speed in single choice emigrations and higher colony cohesion in binary choice emigrations. Additionally, colonies allowed to explore both high and low quality nest sites for one week prior to emigration remained more cohesive, made more accurate decisions and emigrated faster than emigrating naïve colonies. These results show that colonies gather and store information about available nest sites while their nest is still intact, and later retrieve and use this information when they need to emigrate. This improves colony performance. Early gathering of information for later use is therefore an effective strategy allowing *T. albipennis* colonies to improve simultaneously all aspects of the decision-making process – i.e. speed, accuracy and cohesion – and partly circumvent the speed-accuracy trade-off classically observed during emigrations. These findings should be taken into account in future studies on speed-accuracy trade-offs.

INTRODUCTION

Cohesive animal groups often have to make consensual decisions to prevent the group from splitting apart and to preserve the advantages of social life, even though collective decision outcomes may sometimes be sub-optimal for certain group members (Conradt & Roper 2005). Group cohesion, speed and accuracy of decisions are fundamental aspects of consensus decision-making which may greatly affect the fitness of group members (Sumpter & Pratt 2009). However, ensuring accuracy of decisions and maintaining group cohesion require time-consuming phases of both information gathering and pooling to accumulate evidence about the alternatives and ensure effective information flow within the group (Conradt & Roper 2005). As a result, decision accuracy and group cohesion cannot

usually be improved without sacrificing decision speed, and vice versa. Such trade-offs between speed and accuracy are commonplace in animal decision-making and information processing and occur at various scales of biological organisation (Chittka *et al.* 2009; Conradt & Roper 2005; Marshall *et al.* 2009; Marshall *et al.* 2006; Sumpter & Pratt 2009).

Speed-accuracy trade-offs in collective decision-making have recently received considerable attention and many experimental and theoretical studies have attempted to describe such trade-offs, identify their underlying causes and investigate optimal strategies to achieve a suitable compromise between speed and accuracy depending on the context (Chittka *et al.* 2009; Franks *et al.* 2009; Franks *et al.* 2003a; Marshall *et al.* 2009; Marshall *et al.* 2006; Passino & Seeley 2006; Pratt & Sumpter 2006; Scholes & Suarez 2009; Sumpter & Pratt 2009). All these studies shared the common assumption that information gathering should start simultaneously with the decision-making process, and have imposed this constraint experimentally by using naïve subjects. However, in natural conditions, individuals may already have some experience and/or knowledge of the alternatives before a choice has to be made; and this could considerably alter the dynamics and outcome of decisions. In this chapter, the effects of prior knowledge of the environment on speed, accuracy and group cohesion and their trade-offs were experimentally investigated in a collective decision-making process: nest emigration by the house-hunting ant *Temnothorax albipennis*.

Temnothorax ants dwell in fragile nests, such as hollow acorns, twigs or rock crevices, which are highly susceptible to disturbance (Möglich 1978). When their current nest deteriorates, colonies select a new nest site using a well-known sequence of behaviours. After their nest has been destroyed, a minority of workers ('scouts') leave the old nest to look for suitable nest sites. When a scout has deemed a new site suitable, she starts recruiting other scouts to it by tandem running – a slow recruitment method whereby one leader teaches one follower the way from the old nest to the new site (Franks & Richardson 2006). Each recruit then assesses the site independently (Visscher 2007) and may start recruiting as well. The population in the new site therefore gradually increases until it reaches a 'quorum threshold' which triggers full commitment to that site (Pratt *et al.* 2002; Pratt *et al.* 2005; Sumpter & Pratt 2009). Scouts then switch from recruiting by tandem running to carrying nestmates and brood items from the old to the new nest. Carrying (or transport) is a fast recruitment method that allows quick relocation of the colony into its new home (Pratt *et al.* 2005; Sumpter & Pratt 2009). Scouts have been shown to recruit more readily to higher quality than to lower quality nest sites (see e.g. Mallon *et al.* 2001; Robinson *et al.* 2009b). This results in an amplificatory process leading to faster population growth in higher quality sites, in which the quorum threshold is reached earlier than in lower quality sites. As a result,

all or most transport is usually directed towards the best available option (Pratt *et al.* 2005; Sumpter & Pratt 2009).

Several reasons justify the choice of nest relocation in *T. albipennis* as a model system to study the effects of previous knowledge of the environment on group cohesion and speed and accuracy of collective decisions. These parameters are indeed easy to measure in laboratory experiments (see e.g. Franks *et al.* 2003a; Franks *et al.* 2003b). Additionally, when allowed to choose between two available nests of different qualities, colonies display a typical speed-accuracy trade-off and emphasise either speed or accuracy depending on the urgency of the situation (Franks *et al.* 2003a; Marshall *et al.* 2009; Marshall *et al.* 2006; Planque *et al.* 2007; Pratt & Sumpter 2006; Sumpter & Pratt 2009). Finally, Franks et al. (2007b) showed that *T. albipennis* colonies can gather information about available nest sites before emigrating, while their own nest is still intact – a phenomenon known as 'reconnaissance'. In particular, colonies familiarised with low quality nest sites developed an aversion towards these sites and tended to avoid them later when they had to emigrate. However, the authors did not investigate how colony performance (i.e. speed, accuracy and cohesion) may be affected by such aversion; additionally, they were unable to detect a similar phenomenon for high-quality nest sites: colonies familiarised with high quality nest sites showed neither aversion nor attraction towards these sites in later emigrations (Franks *et al.* 2007b).

In this chapter, we re-examined whether *T. albipennis* colonies can gather information about high quality nest sites prior to emigration by using a spatially complex exploration/emigration arena, contrasting with the simple square arena used in the study by Franks et al. (2007b). More specifically, we investigated whether familiarisation with high quality nest sites had an impact on colony performance in terms of emigration speed, nest choice accuracy and group cohesion. We found that familiarisation with a single high quality nest site prior to emigration increased emigration speed in single choice emigrations (*experiment II.1*) and led to biased nest choice and increased group cohesion in binary choice emigrations (*experiment II.2*). We also found that familiarisation with high quality and low quality nest sites prior to emigration led to increased group cohesion and improved both speed and accuracy of emigrations (*experiment II.3*), in apparent contradiction with the classical implications of a speed-accuracy trade-off.

METHODS

Collecting and rearing of colonies

Experiments described in this and all following chapters were performed with colonies of *T. albipennis* collected in Dorset, UK, between 2007 and 2010. Colonies were brought to Bristol, UK, where they were kept in the laboratory as described in Franks *et al.* (2003b). Colonies were housed in artificial nests consisting of a cardboard perimeter sandwiched between two glass slides (50 x 76 mm) with internal cavity of 35 x 50 mm, ceiling height of 1.8 mm and entrance of 2 x 8 mm. They were fed once a week with diluted honey, drosophila and water *ad libitum*. All experiments were performed under natural sunlight, in exploration/emigration arenas consisting of Petri dishes covered with lids and whose walls were coated with Fluon to prevent ants from escaping.

Nests, exploration arenas and general experimental protocol

T. albipennis colonies have been shown to consistently prefer nests with a dark interior over bright nests (Franks *et al.* 2003b). Accordingly, we designed two types of nests of different quality: ‘good nests’ were covered with a top sheet of cardboard so their nest cavity was dark, whereas ‘mediocre nests’ had no such cover and were therefore bright. All experimental nests had a paper floor between the cardboard perimeter and the bottom slide. At the beginning of all experiments, colonies were housed in good nests.

Experiments were performed in geometrically complex, symmetrical exploration arenas consisting of large and small Petri dishes (respectively 22 x 22 x 2.2 cm and 10 x 10 x 1.7 cm) interconnected by tunnels (Figure II.1). Each tunnel was made of two spectrometry cuvets positioned side by side and whose base was cut off to allow ants to walk through them. Tunnels fitted tightly through the walls of adjacent dishes, and any gaps between tunnels and dish walls were filled with silicone. Six conspicuous landmarks painted with black powder paint (two cylinders of 26 mm diameter by 14 mm height; two cones and one inverted cone of 25 mm base and 12 mm height; and one truncated sphere of 18 mm diameter; disposed as shown in Figure II.1) were interspersed in the arena to help the ants orientate. Colonies housed in their old nest were positioned in the middle of the central dish (Figure II.1). Food and water were placed on top of their nest so that their position would not influence exploration pattern.

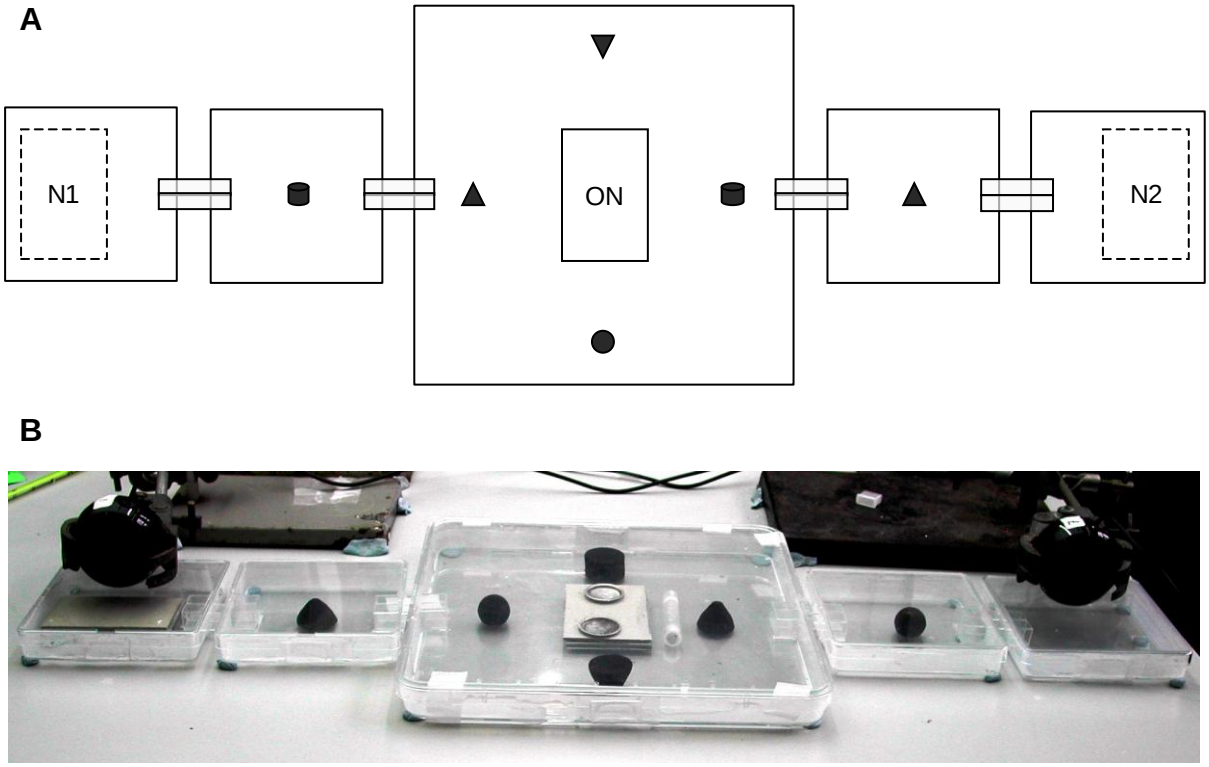

Figure II.1 Experimental design
Top view diagram **(A)** and perspective view **(B)** of an exploration arena. Arenas consisted of one large, central dish; two small, intermediate dishes; and two small, peripheral dishes. Adjacent dishes were connected by tunnels for the ants to walk through. Conspicuous landmarks (black) were used to help ants orientate in the arena. Colonies housed in their old nest (ON) were positioned in the middle of the central dish. One or two available new nest sites (N1 and N2) were positioned in the peripheral dishes either at the onset of exploration (familiar nests) or at the onset of emigration (unfamiliar nests). The position of new nest sites (right or left) was pseudo-randomised between colonies.

Colonies were allowed freely to explore the experimental arena during one week. At the end of exploration, colonies were induced to emigrate by removing the top glass and cardboard perimeter of their old nest. At the onset of emigration, food trays and water tubes were removed from the arena and all workers observed in the intermediate or peripheral dishes were gently taken with soft forceps and released in the central arena. This general experimental protocol was followed in all experiments in this and the following chapters, unless otherwise stated.

Experimental designs

Emigrating colonies were presented with one (experiment II.1) or two (experiments II.2 and II.3) available new nest sites positioned in the peripheral dishes of the arena (Figure II.1). New nest sites were introduced in the arena either at the onset of exploration, so that they could be discovered and visited by individuals for one week before emigration (‘familiar’ nests), or at the onset of emigration, so that they were novel to all individuals in the colony at the time of emigration (‘unfamiliar’ nests).

Experiment	*n*	*n'*	Old nest	Treatment	Available nest sites	
					Exploration	Emigration
II.1	30	24	Good	Naïve	Ø	1 Good (U)
				Informed	1 Good	1 Good (F)
II.2	36	33	Good	Naïve	Ø	1 Good (U) + 1 Good (U)
				Informed	1 Good	1 Good (F) + 1 Good (U)
II.3	24	22	Good	Naïve	Ø	1 Good (U) + 1 Mediocre (U)
				Informed	1 Good + 1 Mediocre	1 Good (F) + 1 Mediocre (F)

Table II-1 Experimental designs
Total number of colonies used in the experiment (n) and in the final data analysis (n'); quality of the old nest; and number and quality of available nest sites during exploration and emigration for each experiment and each treatment (when applicable). For the emigration phase, it is indicated whether new nest sites are familiar (F) or unfamiliar (U).

Three different experiments were run (Table II-1). In experiment II.1, colonies were allowed to emigrate into one good new site under two treatments: in the 'informed' treatment, colonies had familiarised themselves with new site before emigration, whereas in the 'naïve' treatment colonies were unfamiliar with that nest. In experiment II.2, colonies were allowed to choose between two identical good new sites under two treatments: in the 'informed' treatment, colonies had familiarised themselves with one of the two new sites, whereas in the 'naïve' treatment colonies were unfamiliar with both nests. In experiment II.3, colonies were allowed to choose between one good and one mediocre new site under two treatments: in the 'informed' treatment colonies had familiarised themselves with both nests whereas in the 'naïve' treatment colonies were unfamiliar with both nests. At the time of emigration, all individuals were naïve regarding all new nest sites in the treatment 'naïve', whereas in the treatment 'informed', some workers were informed and other were naïve depending on whether they had visited the familiar nest during exploration or not. However, for simplicity, the entire colony will hereafter be referred to as 'naïve' or 'informed' when presenting colony-level results.

As some colonies consistently displayed little activity during the exploration period, we excluded from later analyses those colonies in which no workers were observed in the peripheral dishes or (if applicable) in the familiar nest(s) at the onset of emigration. Additionally, some colonies emigrated into the new sites during the exploration period; those colonies were also excluded from the final analysis. The number of colonies used in the later analyses was therefore 24 in experiment II.1; 33 in experiment II.2; and 22 in experiment II.3 (Table II-1).

In all experiments, colonies were tested each under both treatments. Half of the colonies received the 'naïve' treatment first, whereas the other half received the 'informed'

treatment first. All experiments consisted of successive blocks where 6 to 10 colonies explored and emigrated simultaneously in a single session. In each block there were as many colonies under 'informed' as in the 'naïve' treatment. Blocks involving the same colonies were separated by more than one week to minimise memory of the previous situation, which is not expressed after 6 days (Langridge *et al.* 2004). This time gap between successive blocks was strictly observed in all experiments presented in this and the following chapters.

Data recording and analysis

Emigrations were observed until all new sites were discovered and we noted down the times at which intermediate and peripheral dishes were first entered by a worker. This allowed us to calculate an *approximate crossing time for intermediate dishes* (interval of time between the first entrance in the intermediate dish and the first entrance in the adjacent peripheral dish).

Additionally, all traffic to and from the new sites was recorded throughout emigration using a Webcam (Logitech ® QuickCam ® Communicate Deluxe with 1.3 Mp sensor) positioned above the nest entrance and connected to motion detection software Webcam Zone Trigger Version 2.300 Pro (Omega Unfold. Inc.), so pictures were taken each time an ant entered or left the nest (Figure II.1 B). Webcams were also present during the entire exploration period so that they would not constitute a novel landmark at the time of emigration. Analysis of pictures then allowed us to determine the *emigration time* for each colony (i.e. time interval between the start of emigration and the last transport of a brood item from the old nest to any new nest). Additionally, we determined for each new nest: i) the *discovery time* (interval from the time emigration was started to the time the new nest was first entered by a worker); ii) the *assessment time* (interval from the time the new nest was first entered by a worker to the time the first brood or adult was carried into the new nest); and iii) the *transport time* (interval from the time the first brood or adult was carried into the new nest to the time the last brood was carried into the new nest). Additionally, we counted the *number of successful forward tandem runs* (i.e. tandem runs where both leader and follower successfully entered the new nest). Monitoring all entrances and exits into and from the new nest sites allowed us to determine the *number of workers in each site over time*; we could therefore determine an *approximate quorum threshold* for each nest (maximum population reached in the nest before the first brood or adult was carried).

In experiment II.2 and II.3, we took pictures of both new nest sites immediately after the end of emigration and (in experiment II.3 only) 24 hours after the onset of emigration. A colony was deemed to have chosen a nest only if all brood items were in that nest; otherwise

it was considered split. Additionally, we counted the total number of items (i.e. adults plus brood items) present in each nest using software ImageJ version 1.42q (National Institute of Health, USA). For each colony we then calculated a *choosiness index* (proportion of items observed in a given nest) and a *cohesiveness index* using the following formulas:

$$Choosiness = \frac{n_1}{n_1 + n_2}; Cohesiveness = \left| \frac{n_1 - n_2}{n_1 + n_2} \right|$$

where n_1 and n_2 are the total number of items (i.e. adults and brood) in new nest sites 1 and 2 respectively; choosiness represented the degree of preference for nest site 1 whereas cohesiveness represented the degree of splitting, ranging from 0 (equal split of the colony between both nests) to 1 (choice of one single nest by the entire colony).

In experiment II.3, colonies were monitored for 24 hours after the onset of emigration. For all colonies which had chosen a single nest after 24 hours, we defined a '*Reunification time*' as the time interval between the start of emigration and the last item of brood carried into the chosen nest; this included both colonies which chose a single nest while emigrating and colonies which primarily split, then reunited after emigration. For data analysis, we only considered colonies which reunited in both treatments (n = 18).

Statistical analyses

In this and all following chapters, statistical analyses were performed with software SPSS version 16.0 (SPSS Inc., Chicago IL), R version 2.10.1 and Minitab version 15.1.

Emigration-dynamic variables, quorum thresholds, number of forward tandem runs, choosiness and cohesiveness indexes were compared among treatments and nests using SPSS general linear mixed model procedure (GLMM) with fixed factors 'Treatment', 'New nest site' (if applicable) and their interaction, and random factors 'Block' and 'Colony'. Statistical significance was tested using an Analysis of Deviance with a Type III Sum of Squares method (comparison of the full model to the full model without the factor of interest). Normality and homoscedasticity of residuals were checked using Kolmogorov-Smirnov and Levene's tests, respectively. If residuals were not normally distributed, we applied either log- or power-transformation to the data. In cases where we could not identify any transformation allowing normalisation of residuals we used non-parametric tests.

In experiment II.1, the influence of the number of workers present in the familiar nest at the onset of emigration on quorum threshold and assessment time was investigated for informed colonies using SPSS linear regression and correlation procedures. For the regression, normality of residuals was checked using Kolmogorov-Smirnov tests.

In experiment II.2 and II.3, nest choice patterns were compared between treatments using two-tailed Fisher-Freeman-Halton's exact tests (Freeman & Halton 1951; Weisstein 2010). Within treatments, nest preference was tested using exact binomial tests with a null hypothesis of random choice between both nests. Because there was a high splitting rate, nest preference was also tested using one-sample t-tests (normal samples) or one-sample Wilcoxon tests (non-normal samples) on choosiness indexes, with a null hypothesis of random choice between both nest, i.e. a hypothetical mean or median of 0.5.

RESULTS

Experiment II.1 – Prior Experience and Emigration Speed

Here, colonies emigrated into one good new nest site positioned at one end of the arena; the opposite end, where there was no suitable nest site, was therefore a 'dead end'.

A total of 864 ant visits to the new nest site were analysed over 60 emigrations.

Emigration was significantly faster for informed colonies, which were familiar with the new nest site, than for naïve colonies, which were unfamiliar with the new site (Figure II.2 A; GLMM, treatment: $F_{1,19} = 20.293$, $p < 0.001$). This was due to informed colonies discovering and assessing the new site faster than naïve colonies; by contrast, transport time did not differ between treatments (Figure II.2 A; GLMM, effect of treatment: discovery time, $F_{1,20} = 17.454$, $p < 0.001$; assessment time, $F_{1,20} = 14.750$, $p = 0.001$; transport time: $F_{1,19} = 1.534$, $p = 0.23$).

There were no differences in the crossing times of intermediate dishes leading to the unfamiliar nest and to the dead end for naïve colonies (random exploration; GLMM, LSD post-hoc comparison: $p = 0.53$; Figure II.2 B). Additionally, crossing times of intermediate dishes leading to the dead end for informed colonies were similar to the crossing times observed in naïve colonies (GLMM, LSD post-hoc comparisons, dead-end (informed)/dead-end (naïve): $p = 0.66$; dead-end (informed)/unfamiliar nest (naïve): $p = 0.29$; Figure II.2 B). By contrast, crossing times were significantly shorter for intermediate dishes leading to the familiar nest in informed colonies (GLMM, LSD post-hoc comparisons, $p < 0.05$ in all comparisons; Figure II.2 B). Faster discovery of the new site in the 'informed' treatment was therefore not due to more effective exploration in all directions; rather, specific information on the position of the familiar nest allowed some individuals to head more quickly towards the nest.

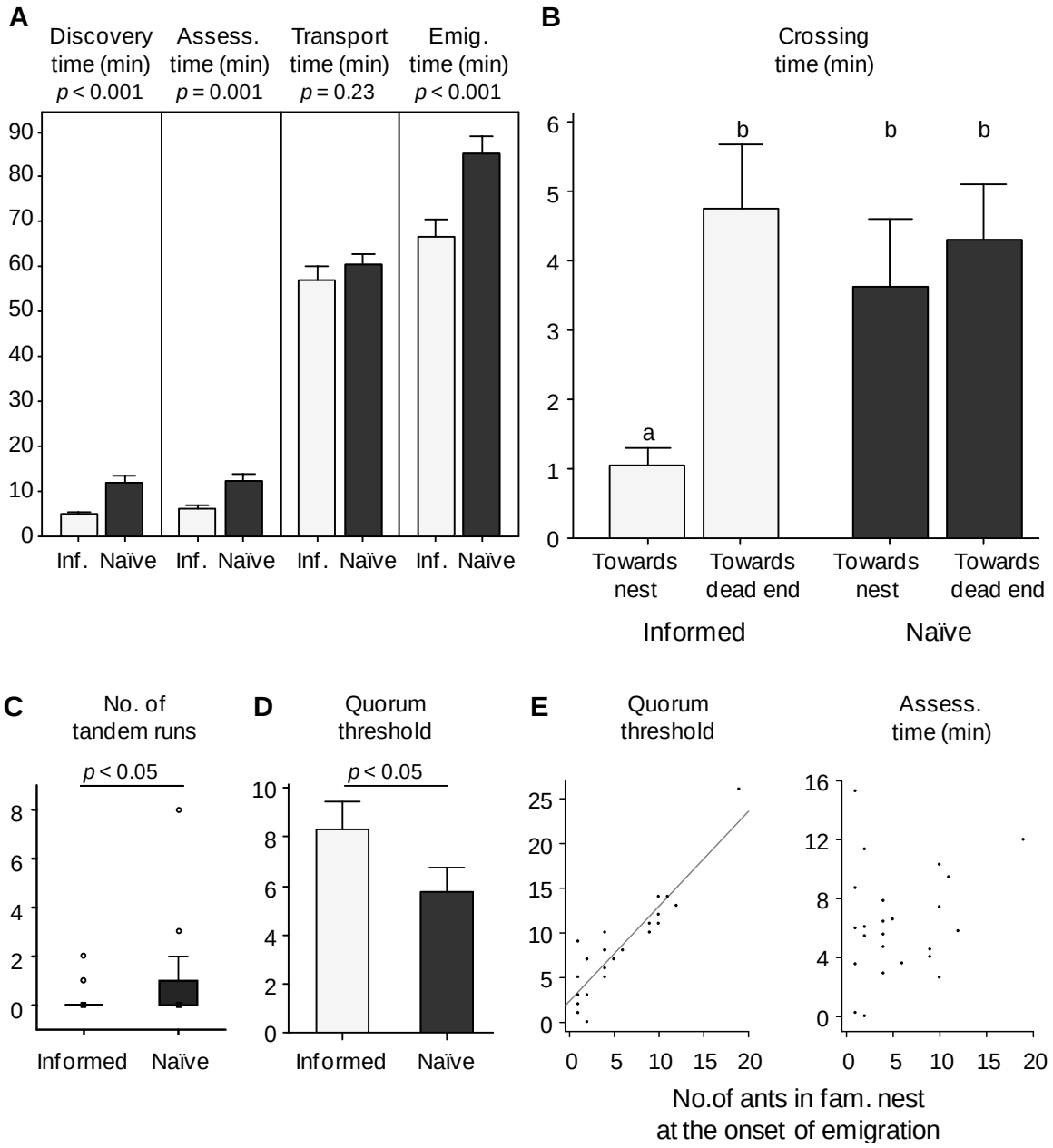

Figure II.2 Prior experience and emigration speed (experiment II.1)
(A-D) Emigration data for informed (Inf., light grey, n = 24) and naïve (dark grey, n = 24) colonies emigrating to a single good nest site. Bars and whiskers represent the means and standard errors, respectively (A-B, D); full squares, rectangles, whiskers and open circles represent the median, interquartile range, 1.5 x interquartile range and outliers, respectively (C). **(A)** Discovery, assessment, transport and emigration times. The effect of treatment on each variable was tested using GLMM (no data transformation). **(B)** Crossing times of intermediate dishes leading either to the new nest site or to the dead-end. Same letters indicate no statistical differences, whereas different letters indicate significant statistical differences ($p < 0.05$) in LSD post-hoc comparisons (GLMM, interaction treatment * direction: $F_{1,64} = 3.688$, $p = 0.059$; no data transformation). **(C)** Number of successful forward tandem runs to the new nest site (Wilcoxon matched-pairs test). **(D)** Quorum thresholds used to switch to transport. The effect of treatment on quorum threshold was tested using GLMM (no data transformation). **(E)** Relationships between the number of ants in the familiar nest at the onset of emigration and, respectively, the quorum threshold (left) or the assessment time (right) for informed colonies (n = 24). Linear regression shows that these relationships are best described by the following equations: (i) Quorum Threshold = 2.422 + 1.059 x No. of ants, $R^2 = 0.82$, $F_{1,22} = 100.814$, $p < 0.001$; and (ii) Assessment time = 5.3 + 0.171 x No. of ants, $R^2 = 0.048$, $F_{1,22} = 1.120$, $p = 0.301$.

During the assessment period, there were fewer forward tandem runs towards familiar nests (informed) than towards unfamiliar nests (naïve; Figure II.2 C; Wilcoxon matched-paired test, Z = -2.2, n = 24, p = 0.028). Nevertheless, the quorum thresholds used in the 'informed' treatment were higher than those used in the 'naïve' treatment (Figure II.2 D; GLMM, effect of treatment: $F_{1,20}$ = 7.305, p = 0.014). This apparent contradiction may be explained because there were usually several workers inside the familiar nest at the onset of emigration. There was indeed a strong correlation between quorum threshold and number of workers in the familiar nest at the onset of emigration for informed colonies (Figure II.2 E; Pearson correlation coefficient r = 0.906, n = 24, p < 0.001). By contrast, we could not detect any correlation between assessment time and number of workers in the familiar nest at the onset of emigration (Figure II.2 E; Pearson correlation coefficient r = 0.220, n = 24, p = 0.3). The faster assessment observed in the 'informed' treatment cannot therefore be solely explained by the presence of workers in the familiar nest at the onset of emigration already constituting a quorum threshold.

Experiment II.2 – Prior Experience, Nest Choice and Cohesiveness

In this experiment, colonies were offered a choice between two identical good new nest sites positioned at either ends of the arena. Informed colonies were familiar with one of these two nests, whereas naïve colonies were unfamiliar with both nests.

Discovery and assessment were significantly faster for familiar than for unfamiliar nests (Figure II.3 A). Additionally, there were significantly fewer forward tandem runs to the familiar than to the unfamiliar nests (Figure II.3 B). Overall emigration time, however, did not differ between informed and naïve colonies (Figure II.3 A). This was due to the high initial splitting rate of colonies (29 out of 33 informed colonies and all naïve colonies (n = 33) split – reunion of split colonies occasionally occurred within 24 hours), which resulted in uneven transport effort between both nests in informed colonies and even transport effort in naïve colonies (Figure II.3 A). The resulting differences in transport time cancelled out the effect of faster discovery and assessment for the familiar nests.

Overall, naïve colonies chose randomly between the two unfamiliar nests (one-sample t-test: t = 1.134, df = 32, p = 0.265) whereas informed colonies showed a significant preference for the familiar nest (one-sample Wilcoxon test: WS = 521, n = 33, p < 0.001); informed colonies were significantly more choosy than naïve colonies (Figure II.3 C; GLMM, effect of treatment on choosiness: $F_{1,14}$ = 12.636, p = 0.003). Additionally, informed colonies were significantly more cohesive than naïve colonies (Figure II.3 C; GLMM, effect of treatment on cohesiveness: $F_{1,14}$ = 18.591, p = 0.001).

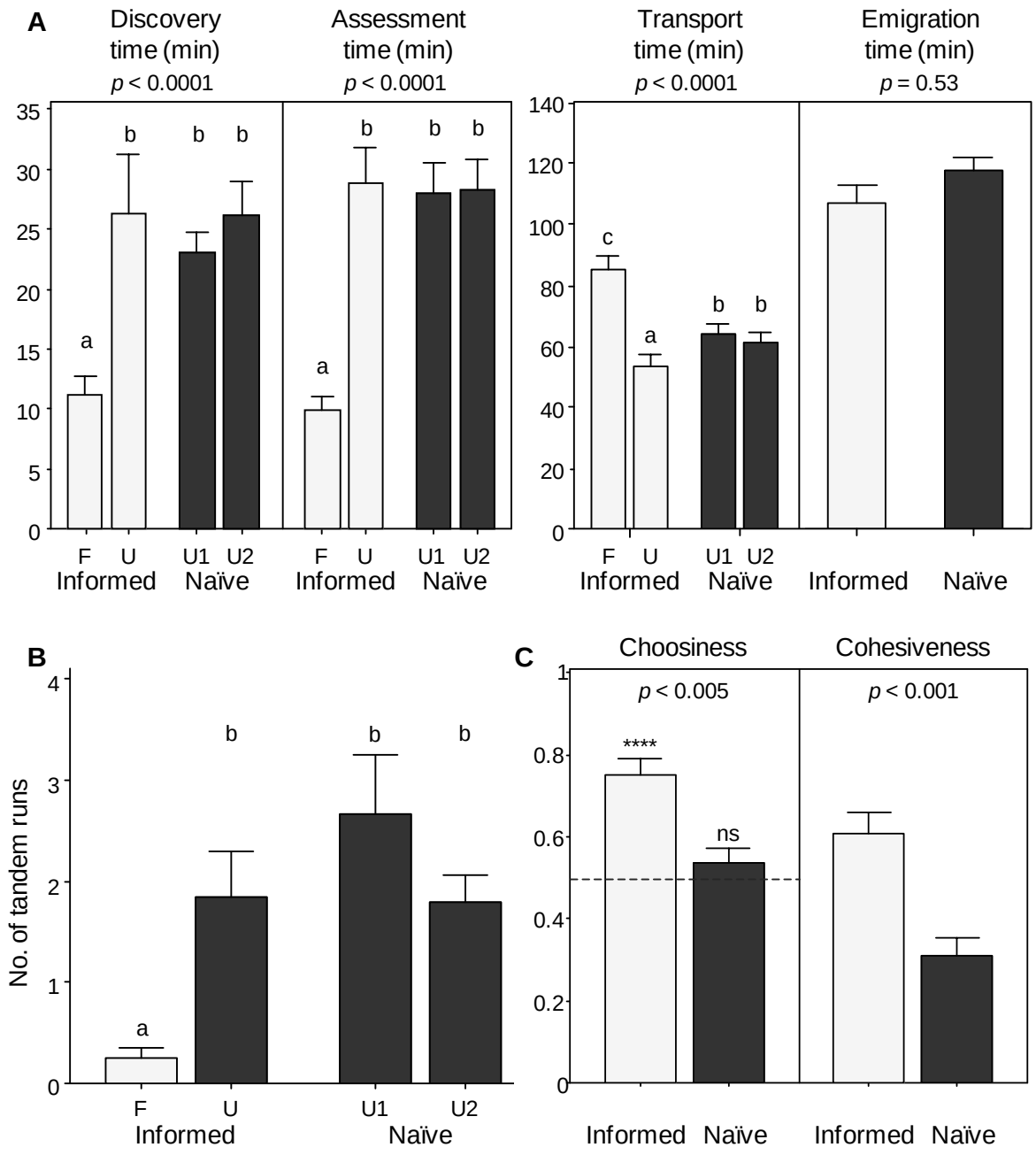

Figure II.3 Prior experience, nest choice and cohesiveness (experiment II.2)
Emigration data for informed (light grey, n = 33) and naïve (dark grey, n = 33) colonies emigrating to a familiar (F) and an unfamiliar (U) good nest or to two unfamiliar good nests (U1 and U2), respectively. Bars and whiskers represent the means and standard errors, respectively. **(A)** Discovery, assessment, transport and emigration times. *P*-values are given for the effect of nest site (familiar/unfamiliar) on discovery, assessment and transport times, and the effect of treatment (naïve/informed) on emigration time (GLMM; discovery time was log-transformed). Same letters indicate no differences, whereas different letters indicate significant differences ($p < 0.05$) in LSD post-hoc comparisons. **(B)** Number of forward tandem runs towards new nest sites. Same letters indicate no differences, whereas different letters indicate significant differences ($p < 0.05$) in LSD post-hoc comparisons (GLMM; effect of nest: $F_{2,76} = 6.877$, $p < 0.005$; no data transformation). **(C)** Choosiness and Cohesiveness indexes. Choosiness was calculated as the proportion of items in the familiar nest (informed colonies) or in U1 (naïve colonies). *P*-values are given for the effect of treatment on both variables (GLMM; no data transformation). The broken line over choosiness – set at 0.5 – represents expectations under the hypothesis of random choice between both nests (*****: $p < 0.001$ in one-sample Wilcoxon test for non-normal data, n = 33; ns: non-significant in one-sample t-test for normal data; df = 32).

Experiment II.3 – Prior Experience and Speed-Accuracy Trade-Off

In this experiment, colonies were offered a choice between one good and one mediocre new nest site positioned at either end of the arena. Informed colonies were familiar with both nests, whereas naïve colonies were unfamiliar with both nests. A total of 1470 ant visits to the new nest sites were analysed over 48 emigrations.

Emigration was significantly faster for informed than for naïve colonies (Figure II.4 A; GLMM, effect of treatment: $F_{1,18} = 6.648$, $p = 0.019$). Familiar nests (both mediocre and good) were discovered earlier than unfamiliar nests (Figure II.4 A; GLMM, effect of treatment: $F_{1,60} = 14.363$, $p < 0.001$). Assessment took longer for mediocre nests than for good nests; additionally, assessment of familiar good nests was faster than assessment of unfamiliar good nests (Figure II.4 A). Because transport started earlier for good than for mediocre nests, but ended simultaneously when all brood items had been carried away from the old nest, transport time was significantly longer for good than for mediocre nests (Figure II.4 A).

At the end of emigration, nest choice pattern did not differ between informed and naïve colonies (Figure II.4 C; Fisher-Freeman-Halton's test: $p = 0.2$). However, there was a significant preference by colonies for good over mediocre nests in the 'informed' treatment (binomial test: $p = 0.002$) but not in the 'naïve' treatment (binomial test: $p = 0.22$). Additionally, taking into account data on split colonies showed that both informed and naïve colonies preferred good nests (Figure II.4 B; one-sample Wilcoxon tests, test: WS = 251, n = 22, $p < 0.001$; naïve: WS = 208.5, n = 22, $p = 0.008$), but informed colonies did so significantly more than naïve colonies (Figure II.4 B; GLMM, effect of treatment: $F_{1,18} = 6.916$, $p = 0.017$). In other words, informed colonies were better at selecting the better option than naïve colonies. Informed colonies tended to be more cohesive than naïve colonies, although this was marginally non-significant (Figure II.4 B; GLMM, effect of treatment: $F_{1,18} = 4.003$, $p = 0.061$).

During emigrations, informed colonies which had familiarised themselves with both the good and the mediocre nests were therefore (i) faster and (ii) more accurate than naïve colonies which were unfamiliar with both nests.

After 24 hours, all informed colonies (n = 22) had chosen the good nest whereas only 17 out of 22 naïve colonies had chosen the good nest (Figure II.5 A; Fisher-Freeman-Halton's exact test: $p = 0.049$). Additionally, reunification time was significantly shorter for informed than for naïve colonies (Figure II.5 B; GLMM, effect of treatment: $F_{1,14} = 7.481$, $p = 0.016$). Informed colonies were therefore able to reunite faster and more successfully than naïve colonies.

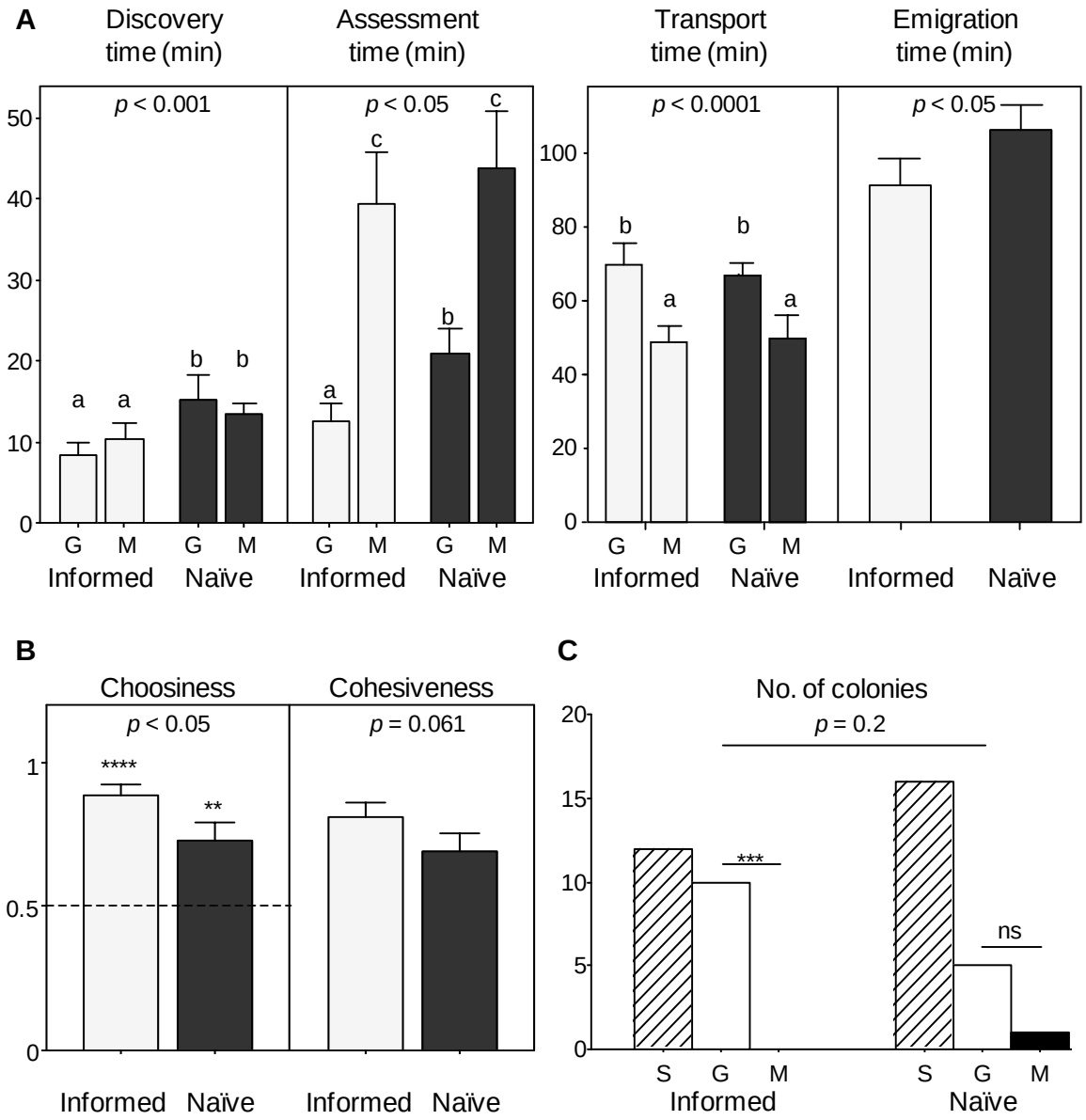

Figure II.4 Prior experience and speed-accuracy trade-off (experiment II.3), emigration
(A-B) Emigration data for informed (light grey, n = 22) and naïve (dark grey, n = 22) colonies emigrating to one good (G) and one mediocre (M) nest sites (experiment II.3). Bars and whiskers represent the means and standard errors, respectively. **(A)** Discovery, assessment, transport and emigration times (discovery, assessment and transport are considered for each site whereas emigration time is considered for each colony). P-values are given for the effects of: (i) interaction between nest quality and treatment on assessment time; (ii) nest quality on transport time; and (iii) treatment on discovery and emigration times (GLMM; discovery and assessment times were log- and power-transformed, respectively). Same letters indicate no statistical differences, whereas different letters indicate significant statistical differences ($p < 0.05$) in LSD post-hoc comparisons. **(B)** Choosiness and Cohesiveness indexes. Choosiness was calculated as the proportion of items in the good nest. Cohesiveness was calculated as described in the Materials and Methods section. P-values are given for the effect of treatment on both variables (GLMM; choosiness was power-transformed). The broken line over choosiness – set at 0.5 – represents expectations under the hypothesis of random choice between both nests (****: $p < 0.001$; **: $p < 0.01$ in one-sample Wilcoxon tests, n = 22). **(C)** Number of colonies splitting (S, hashed bars) or choosing the good (G, white bars) or mediocre nest (M, black bars) at the end of emigration. Nest choice patterns were compared between treatments using Fisher-Freeman-Halton's exact test and nest preference was tested within each treatment using exact binomial tests (ns: non-significant; ****: $p < 0.001$).

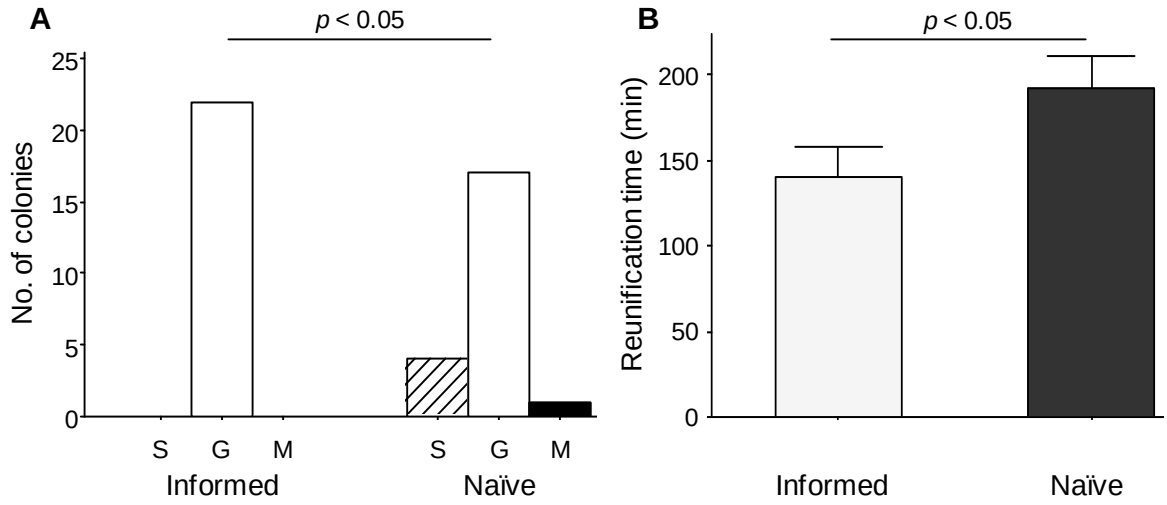

Figure II.5 Prior experience and speed-accuracy trade-off (experiment II.3), final state
(A) Number of colonies split (S, hashed bars) or having chosen the good (G, white bars) or mediocre nest (M, black bars) 24 hours after emigration onset. Nest choice patterns were compared between treatments using Fisher-Freeman-Halton's exact test and nest preference was tested within each treatment using exact binomial tests (ns: non-significant; ****: $p < 0.001$). **(B)** Reunification time for informed (light grey, n = 18) and naïve (dark grey, n = 18) colonies. Bars and whiskers represent the means and standard errors, respectively. The effect of treatment on reunification time was tested using GLMM (no data transformation).

DISCUSSION

Our results show that colonies of *T. albipennis* gather information about the location of available good nest sites prior to emigration, while their own nest is still intact, and can later retrieve and use that information when they have to emigrate. In all experiments, emigrating colonies indeed discovered familiar good nest sites faster than sites they had never encountered before. This was due to directed, i.e. non-random, exploration towards familiar sites. Additionally, assessment times (time interval between the first discovery of a nest and full commitment to that nest) were shorter, and workers led fewer tandem runs, for familiar than for otherwise identical unfamiliar good nest sites. This indicates that at the onset of emigrations, colonies already had information on the suitability of high quality nest sites they had familiarised themselves with.

These results confirm that reconnaissance and prior experience affect nest emigration in *T. albipennis*, as previously shown in several studies (Franks *et al.* 2007b; Healey & Pratt 2008). However, the observation that colonies learnt the location and suitability of good nest sites contrasts with a previous study by Franks et al. (2007b), who were unable to detect an effect of familiarisation with good nest sites on colony performance. This is because in that study, the exploration arena used was small and geometrically simple (22 x 22 cm dish). As a result, both familiar and unfamiliar nests were easy to find and there was little benefit in previous exploration of the familiar nest. By contrast, the exploration

arena used in the present study was geometrically more complex (Figure II.1; one 22 x 22 cm dish was connected at opposite ends to two intermediate and two peripheral 10 x 10 cm dishes via a series of 4 cm long tunnels). This made new nest sites more difficult to find as they were separated from the old nest by two narrow tunnels. The advantages derived from previous knowledge of the location of the familiar nest should therefore be much higher, explaining the difference between this and previous studies.

Gathering information on high quality sites prior to emigration had a strong impact on colony performance during emigrations, i.e. on group cohesion, emigration speed and decision accuracy. When only one good new nest was available (experiment II.1), colonies that had previously been in contact with that nest emigrated faster than naïve colonies. When there was a choice between two identical good new nests (experiment II.2), colonies which had previously been in contact with one of these two nests showed a clear preference for that nest and remained more cohesive than naïve colonies, which chose randomly between both nests. Experiments II.1 and II.2 therefore showed that familiarisation with a high quality nest could improve emigration speed and group cohesion independently, but did not reveal how both parameters could be affected simultaneously. In experiment II.3, we allowed to colonies to choose between a good and a mediocre nest. Colonies which were familiar with both nests were faster, better at selecting the good nest and were marginally more cohesive than naïve colonies, both during the emigration process and at long term. In these specific experimental conditions (arguably more realistic than those in experiments II.1 and II.2, because colonies in their natural environment should encounter several suitable nesting cavities of different qualities) gathering information prior to emigration therefore allowed to improve simultaneously speed, accuracy and group cohesion.

These results are quite striking, as speed and accuracy of *T. albipennis* emigrations have repeatedly been shown to be subject to a trade-off, i.e. nest choice accuracy (and group cohesion) cannot be improved without having to spend more time in the decision-making process. The existence of such constraint on *T. albipennis* emigrations has received much support, both experimentally and theoretically (Chittka *et al.* 2009; Franks *et al.* 2009; Franks *et al.* 2003a; Marshall *et al.* 2009; Marshall *et al.* 2006; Planque *et al.* 2007; Pratt & Sumpter 2006; Sumpter & Pratt 2009) and is in keeping with the presence of similar speed-accuracy trade-offs in emigrations by other house-hunting social insects (ants: Scholes & Suarez 2009; bees: Passino & Seeley 2006). Speed-accuracy trade-offs are widespread in living organisms and affect all levels of biological organisation (Chittka *et al.* 2009), from information processing in cells and nervous systems (Marshall *et al.* 2009; Reddi & Carpenter 2000; Skorupski & Chittka 2010; Skorupski *et al.* 2006; Trimmer *et al.* 2008) to decision-making in individuals (Burns & Dyer 2008; Burns & Rodd 2008; Chittka *et al.* 2003;

Spaethe *et al.* 2001; Trimmer *et al.* 2008) and groups of individuals (Chittka *et al.* 2009; Conradt & Roper 2005); this is because gathering information in order to reach a decision is a time-consuming, noisy process, and increasing the accuracy of decision requires to spend more time accumulating evidence. Because the inherent property of a speed-accuracy trade-off is that one parameter cannot be improved without sacrificing the other, animals need to find a good compromise between both parameters depending on the costs incurred by inaccurate choices and/or slow decisions. Strategies for decision-making may therefore vary between individuals (or groups of individuals) (Burns & Dyer 2008; Burns & Rodd 2008; Chittka *et al.* 2003; Muller & Chittka 2008), but may also vary within a single individual (or group of individuals), depending on the context, to meet the requirements of specific situations by emphasising either speed or accuracy (Chittka *et al.* 2003; Chittka *et al.* 2009; Franks *et al.* 2003a; Spaethe *et al.* 2001). Here, however, *T. albipennis* colonies appear to apply a strategy (i.e. gathering information long before the start of the decision-making process) which allows them to improve both parameters simultaneously.

The gap in time between information collection and exploitation is the key to improving both speed and accuracy of emigrations in *T. albipennis*: colonies indeed pay most of the time costs of discovering and assessing nests in advance, while their nest is still intact, which allows decisions to be both swift and accurate later if and when they need to emigrate. Time gaps between gathering and exploiting information have already been described in solitary species, such as prospecting birds (Danchin *et al.* 2001) and parasitic wasps (Collett 2008). In both cases, this phenomenon derives mainly from important time constraints on information availability. Prospecting birds, for example, inspect various breeding patches and assess the reproductive success of conspecifics using social cues at the end of the breeding season. This influences their settlement choice in the next year: most prospecting birds choose to settle closer to higher quality patches. The reason for such early prospecting is that the best cues for predicting breeding patch quality are social cues, which are not present at the time of the settlement but can only be monitored at the end of the previous breeding season (Danchin *et al.* 2001; Doligez *et al.* 2004; Part & Doligez 2003; Ward 2005). Parasitic wasps are also subjected to time constraints. *Hyposoter horticola*, for example, needs to oviposit into its host's eggs at a very specific, short duration developmental stage. Similarly, parasitic wasps *Argochrysis armilla* need to enter nests of digger wasps *Ammophila* sp. in the brief period between their host bringing a caterpillar back to its nest and sealing it. As the period during which oviposition is possible is very short and therefore precludes search at that stage, these parasitic wasps need to learn the location of their hosts' eggs or nests in advance and monitor them regularly (Collett 2008). Such time constraints on information availability may explain why solitary species may gather information well before they need to

use it, in spite of the high potential costs incurred by such early search. Any time and energy spent on searching is indeed diverted from present reproduction and maintenance, which may have substantial fitness costs (Danchin *et al.* 2001; Stamps *et al.* 2005; Sullivan 1994). However, these costs should be compensated for because early gathering of information is likely to greatly enhance future reproduction (Collett 2008; Danchin *et al.* 2001).

This situation contrasts with that of *T. albipennis* ants, which are not subject to time constraints on information availability. In natural conditions, suitable nest sites are indeed permanently accessible to workers, and nest site quality is best predicted by its present physical properties such as light level, headroom and entrance width (Franks *et al.* 2003b). Additionally, naïve colonies have been repeatedly shown to be able to assess, choose and relocate effectively to new nest sites during an emigration, even if they have never encountered these sites before (Franks *et al.* 2006a; Franks *et al.* 2007a; Franks *et al.* 2006b; Franks *et al.* 2008; Franks *et al.* 2005; Franks *et al.* 2007c; Franks *et al.* 2003b; Mallon *et al.* 2001; Robinson *et al.* 2009b). There is therefore no absolute necessity for colonies to gather information about nest sites prior to emigration. Even more strikingly, contrary to the solitary species mentioned above, which are preparing for a certain event (future reproduction), *T. albipennis* colonies gather information for later emigrations, which are uncertain events: an emigration may indeed not occur at all if the nest remains intact throughout the season (Möglich 1978). Why, therefore, pay the costs of early information gathering (Dornhaus *et al.* 2006) if the benefits associated with it are limited and may never be obtained? One answer is that even though the need for emigration may be unpredictable, they are probably quite frequent in *Temnothorax* species, especially those living in temporary nests such as hollow acorns and twigs. Additionally, the social organisation of ants colonies, based on division on labour (Blanchard *et al.* 2000; Dornhaus *et al.* 2009; Franks & Sendova-Franks 2000; Hölldobler & Wilson 1990; Robinson *et al.* 2009a), reduces considerably the costs associated with information gathering while the nest is still intact. Exploration of available nest sites may indeed be time consuming and require energy, but it can be carried out with little extra cost by the same individuals that go out of the nest on a daily basis to explore and perform indispensable tasks such as foraging and patrolling. Visiting and assessing nest sites by patrollers and/or foragers while the nest is still intact should therefore be less costly – in terms of both time and energy – than during emergency emigrations, where it involves considerable efforts by many individuals (up to a 40% of a colony's total workforce; see Franks *et al.* 2009). Additionally, the potential consequences of time delays differ drastically between the two situations: while the nest is intact, most of the colony (and especially the queen) is safe inside the nest and can be effectively defended by a few individuals positioned at the entrance (Franks *et al.* 2003b). By contrast, during emergency

emigrations, the entire colony is exposed so any time delays associated with information gathering may increase risk and incur higher costs to the vulnerable colony (Franks & Sendova-Franks 2000). Gathering information while the nest is still intact should therefore greatly increase colony performance during later emigrations by simultaneously improving emigration speed, decision accuracy and group cohesion at relatively low costs and risks.

Our results imply that information about available nest sites is continually gathered by exploring individuals while the nest is still intact, then retrieved and shared among scouts during emigrations, thus affecting collective performance. Information about suitable sites should therefore be available at any time and relatively easy to transfer among colony members. A previous study by Franks et al. (2007b) suggested that both chemical marking and visual cues may be involved in storing and retrieving information about low quality nest sites. Similarly, chemical marking and/or memory by informed individuals could play an important role in retrieving information about high quality nest sites. Other social cues (such as interactions among workers in new nest sites) could also be partly responsible for the faster assessment of high quality nest sites we observed in our experiments: in most cases a few workers were stationed inside good familiar nest sites at the onset of emigrations; these workers could help reach the quorum threshold faster than if the site was empty. However, although the number of workers present in the nest at the onset of emigration was strongly correlated with the quorum threshold, we did not find any evidence that it had an influence on assessment time. Further investigations will be necessary to determine what form(s) of information is (are) stored and the relative roles of informed versus naïve individuals in emigrations to high-quality, familiar nest sites (see Chapter IV, p53, and Chapter V, p69).

Emigrations by *Temnothorax* ants represent one of the main sources of inspiration for theoretical models on speed-accuracy trade-offs in collective decision-making, aiming at identifying the sources of such trade-offs and possible optimal strategies to compromise between speed and accuracy (Chittka *et al.* 2009; Marshall *et al.* 2009; Marshall *et al.* 2006; Planque *et al.* 2007; Pratt & Sumpter 2006; Sumpter & Pratt 2009). However, all these models consider that colonies are totally naïve at the beginning of emigrations. The present study shows that in natural conditions, this may not be the case, as colonies are able to store information about available nest sites of different quality prior to emigration, then retrieve and use that information during emigrations, which in some cases allows improving both speed and accuracy of the decision-making process. We believe that previous knowledge of the environment should be taken into account in theoretical as well as experimental work on speed-accuracy trade-offs in collective decision-making, and hope the present work will stimulate new studies considering this issue.

This Chapter presented empirical evidence that emigrating colonies collectively benefit from prior familiarisation with high-quality, available nest sites. It is also known that colonies develop an aversion towards low-quality, familiar nest sites, but the impact on colony performance of such aversion is not known (Franks *et al.* 2007b). The next Chapter will be aimed at investigating this issue, with particular regard to the flexibility of collective choices and the adjustment of decisions to local conditions.

Chapter III. Experience-Dependent Flexibility in Collective Decision-Making by House-Hunting Ants

ABSTRACT

When making a decision, solitary animals often adjust to local conditions by using flexible evaluation and decision criteria, even though these may occasionally lead to irrationality. By contrast, collective decision-making in large animal groups – such as nest choice by emigrating ant colonies – is usually considered to rely on robust, fixed preference rules and to be immune to irrationality. Here, we show that familiarisation with available nest sites prior to emigration can lead to flexible collective decisions in the house-hunting ant Temnothorax albipennis. Colonies allowed to inspect a mediocre nest site while their home nest is still intact usually develop an aversion towards that nest. We found that aversion strength did not depend on the absolute quality of the familiar nest, but on its quality relative to the home nest. As a result, nest choice in later emigrations depended strongly on the quality of the previously experienced home nest, allowing colonies to adjust to the local quality of available sites. Additionally, we found that in a worst-case scenario where the only alternatives are of even lower quality, developing an aversion towards a mediocre nest can occasionally lead to poor collective decisions. We discuss whether the observed flexibility in collective choices necessarily requires experience-dependent changes in individual decision criteria, and develop a new analytical model of nest choice in house-hunting ants showing that a fixed-threshold decision strategy at the individual level can lead to experience-dependent, flexible decisions at the colony level.

INTRODUCTION

Animals are often faced with choices that may have an important impact on their fitness, e.g. while foraging (Pyke 1984), selecting a mate (Bateson 1983) or a new habitat (Clobert *et al.* 2001; Johnson & Gaines 1990). In theory, animals could increase their fitness by selecting the best available option; however, gathering information about alternatives takes time and energy and can be risky, so delaying decision-making in order to make the best choice could be costly (Dechaume-Moncharmont *et al.* 2005; Luttbeg 1996; Stamps *et al.* 2005; Sullivan 1994). Many theoretical studies have investigated optimal strategies for searching, evaluating candidates and making a decision under time constraints, especially in the context of mate choice (Bateson & Healy 2005; Collins *et al.* 2006; Luttbeg 1996; Stamps *et al.* 2005; Sullivan 1994; Ward 1987).

Decision-making strategies can be divided into two main categories: absolute evaluation of options with threshold-based decision criteria (accept any satisficing candidate, e.g. above a minimum quality requirement, or threshold, stored internally; otherwise keep searching; see e.g. Collins *et al.* 2006; Collins 1995; Ferguson 1989; Moore & Moore 1988;

Real 1990; Reid & Stamps 1997), or relative evaluation of options with comparative decision criteria (e.g. choose the best of all visited alternatives (*best-of-n* strategy); or compare successive pairs of options (*sequential comparison* strategy); see e.g. Bakker & Milinski 1991; Bateson & Healy 2005; Luttbeg 1996; Sullivan 1994).

In temporally and spatially varying environments, search strategies and decision criteria need to be flexible to allow efficient decision-making in various circumstances: indeed, having too high standards in a low quality patch may lead to decisions being unnecessary delayed, whereas having too low standards in a high quality patch may lead to hasty, sub-optimal choices. Taking into account the quality of other alternatives while assessing a given option should therefore confer crucial fitness benefits on individuals (Collins *et al.* 2006) and has been observed in mate choice in insects (crickets: Wagner *et al.* 2001; fruit flies: Dukas 2005; bark beetles: Reid & Stamps 1997), fish (sticklebacks: Bakker & Milinski 1991) and birds (zebra finches: Collins 1995) among others. Such flexibility in evaluation and decision criteria is inherent to comparative strategies, but can also be achieved in threshold-based strategies through pre-assessment of local patch quality (Reid & Stamps 1997) or step-by-step adjustment of acceptance thresholds during successive visits of candidates (Collins *et al.* 2006).

Taking into account other alternatives while assessing an option has however been shown occasionally to lead to irrationality. In economics, the theory of rational choice states that preference between two options with given utility values should be consistent across contexts (Doyle *et al.* 1999; Simon 1955; Tversky & Kahneman 1981; Tversky & Simonson 1993). This concept has been extended to the study of animal decision-making: an animal is considered rational if its preference between two options with stable fitness-related values is consistent across contexts (Bateson & Healy 2005; Houston *et al.* 2007; Schuck-Paim *et al.* 2004; Waite 2001). In particular, rationality implies that choices should be transitive (e.g. if option *a* is preferred to *b* and *b* to *c*, then *a* should be preferred to *c*) and independent of irrelevant alternatives (i.e. the relative preference for an option *a* over an option *b* should not be modified by the presence of a third option *c* or 'decoy'; (Bateson & Healy 2005; Schuck-Paim *et al.* 2004). Violations of the rational choice theory have, however, been reported multiple times in humans (see e.g. Doyle *et al.* 1999; Tversky & Kahneman 1981) and animals (see e.g. Bateson & Healy 2005; Houston *et al.* 2007; Schuck-Paim *et al.* 2004), and can be brought about by variations in the local context (e.g. adding an additional option to a choice set may induce changes in the relative preference between other options; Bateson & Healy 2005; Doyle *et al.* 1999; Tversky & Simonson 1993) or in the background context (i.e. options encountered in the past may induce changes in the relative preference between current options; see Schuck-Paim *et al.* 2004; Tversky & Simonson 1993; Waite 2001). Such

irrationality in individuals is usually considered as evidence for cognitive illusions due to comparative evaluation of the alternatives (Schuck-Paim *et al.* 2004; Waite 2001). However, such deviations may also reflect adaptive adjustments to local conditions, or represent a mere side-effect of decision heuristics that usually perform well in an animal natural's environment (Houston *et al.* 2007).

The issues of flexibility in decision criteria and irrationality have been well studied in solitary animals, but have received much less attention in collective decision-making (Edwards & Pratt 2009). In animal groups, decisions made by individuals on the basis of their own information have to be collated and integrated to produce a common decision at the group level (Conradt & Roper 2005; King & Cowlishaw 2007). Because decision rules may differ greatly at the group and at the individual levels, decision-making strategies used by individuals may not be directly reflected by the apparent collective strategy. This is particularly striking in the case of nest choice by colonies of house-hunting ants, which are able to select the best among several available nest sites (apparent *best-of-n* comparative strategy at the group level; see Franks *et al.* 2006a; Franks *et al.* 2003b) without necessarily requiring individuals to visit and compare all options (Robinson *et al.* 2009b). There is therefore much scope for research on the links between individual and collective strategies for decision-making in animal groups, and their impact on the flexibility and rationality of choices.

House-hunting by ants of the genus *Temnothorax* is a good model system to study such issues, as the interplay between individual and collective decision-making during emigrations has been thoroughly investigated (Franks *et al.* 2002; Marshall *et al.* 2009; Marshall *et al.* 2006; Pratt *et al.* 2002; Pratt & Sumpter 2006; Pratt *et al.* 2005). Emigrating *Temnothorax* colonies have been shown to behave rationally when choosing between two unknown nest sites in the presence or absence of an irrelevant decoy (Edwards & Pratt 2009), contrasting with several instances of decision-making by solitary animals (Bateson & Healy 2005). This suggests that criteria for nest preference are stable at the colony level, in agreement with previous studies showing high consistency in nest preference among colonies and over time (Franks *et al.* 2003b). However, recent studies showed that nest choice in *T. albipennis* can be altered by prior familiarisation with some or all available nest sites (see Franks *et al.* 2007b and Chapter II). In particular, colonies which familiarised themselves with a mediocre nest site prior to emigration developed an aversion towards that nest, and avoided it in later emigrations (Franks *et al.* 2007b). Here we investigated whether this familiarisation process could allow ant colonies to adjust their acceptance criteria to the local distribution of available nests, and whether this might lead them to apparent irrationality in certain conditions.

In a first experiment, we show that developing an aversion towards a mediocre nest site can induce poor decisions if the only other alternative is of even lower quality, although most colonies are able to overcome their initial aversion and select the better option. In a second experiment, we show that the intensity of aversion towards a mediocre nest site does not depend on the absolute quality of that site, but on its quality relative to the current nest. We then discuss three possible decision-making strategies that may account for our results: (i) direct comparisons by individuals; (ii) adjustment of individual acceptance threshold through experience of the current nest; and (iii) fixed individual acceptance thresholds leading to flexibility at the colony level. Because the latter possibility has never been theoretically investigated before, we develop a two-stage analytical model exploring in which conditions this scenario could account for our results.

METHODS

Four types of artificial nests ranging from high to very low quality were used (Table III-1). Experiments were performed in large Petri dishes (22 x 22 x 2.2 cm). Emigrating colonies could choose between two equidistant available nest sites, either familiar (i.e. previously explored by workers) or unfamiliar (i.e. never encountered before), and whose position relative to the old nest (left or right) was pseudo-randomised between trials (Figure III.1). Nest choice was recorded after 24 hours.

	Brightness	Headroom (mm)	Entrance width (mm)
Good nest type 1	dark	1.8	2
Good nest type 2	dark	1.1	2
Mediocre nest	bright	1.1	2
Poor nest	bright	1.1	20

Table III-1 Characteristics of different types of nest

Experiment III.1 – Aversion and nest choice accuracy

Colonies housed in good old nests (type 2) were induced to emigrate and choose between a mediocre and a poor nest (Table III-1) under two treatments. In the 'Informed' treatment, colonies were allowed to examine the mediocre nest for one week prior to emigration, whereas the poor nest was introduced in the arena at the onset of emigration. These colonies therefore had a choice between one mediocre, familiar nest, and one poor, unfamiliar nest. In the 'Naïve' treatment, colonies were allowed to acclimatise to the exploration arena for 24 hours – time enough for *Temnothorax* ants to familiarise themselves with a novel environment (Aron *et al.* 1986). Both mediocre and poor nests were then simultaneously introduced in the arena at the onset of emigration. These colonies therefore had a choice between two unfamiliar nests. Twenty colonies were tested each under both treatments ('Naïve' then 'Informed').

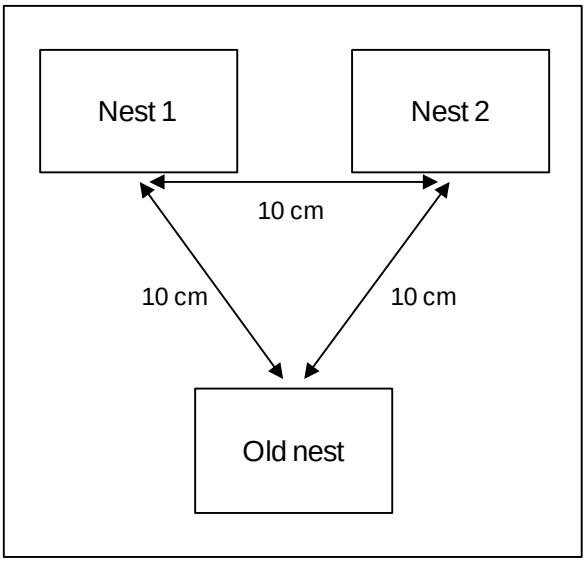

Figure III.1 Experimental design
Colonies housed in their old nest were positioned along one side of the exploration arena. After an acclimatisation/exploration period, emigration was induced and colonies were allowed to choose between two equidistant nests (Nests 1 and 2) placed along the opposite side of the arena. The quality (poor or mediocre) and status (familiar or unfamiliar) of nests 1 and 2 varied between experiments; in each experiment, the position of both nests (left or right) was pseudo-randomised.

Experiment III.2 – Old nest quality and aversion intensity

Colonies housed in either a mediocre (treatment 1) or a good nest (type 1, treatment 2) were allowed to examine a mediocre nest (‘familiar nest’) for 6 days prior to emigration. Another mediocre nest (‘unfamiliar nest’) was then introduced in the arena at the onset of emigration. Colonies therefore had a choice between one familiar and one unfamiliar, otherwise identical, mediocre nest.

Twenty colonies were tested each under both treatments; ten colonies were first exposed to treatment 1, whereas the others were first exposed to treatment 2.

To relate nest choice to exploration intensity, we recorded for each colony the number of workers present in the familiar nest daily at a fixed time. Observations were carried out at 14h00 on every day of exploration (except on the third day), and at the onset of emigration. Additionally, 18 colonies were observed continuously for one hour each during exploration to record the number of workers entering and leaving the familiar nest during this period. Observation bouts were evenly spread throughout the exploration period, subject to day and time of observation being kept identical under both treatments for each colony.

Statistical analyses

Nest choice patterns were compared between treatments using two-tailed Fisher's exact tests. Within treatments, nest preference was tested using exact binomial tests with a null hypothesis of random choice between both nests.

In experiment III.2, the number of workers present in the familiar nest on daily scans was analysed using a generalised linear mixed model (GLMM) with gamma error distribution, implemented using the function glmmPQL from R package MASS. The model included colony as a random effect. We selected the model fitting our data best by using a stepwise backward procedure. Statistical significance was evaluated by applying z-tests to parameter estimates in fitted models. The final selected model included the significant effects 'treatment', 'colony size', and 'day of observation'.

The number of entries and exits in/from the familiar nest during an observation bout was compared between treatments using paired t-tests on log-transformed data. Normality of data after transformation and equality of variances were checked using respectively Shapiro-Wilk's tests (n = 18, $p > 0.100$ for all samples) and F-tests (Entries: $F_{17,17} = 0.58$, $p = 0.266$; Exits: $F_{17,17} = 0.71$, $p = 0.496$).

Modelling

We considered a scenario where each individual ant has an internal threshold for nest acceptance. There may be inter-individual variation in thresholds within a colony, but thresholds are assumed not to vary over time. We developed a two-stage model (Figure III.2) to investigate whether the flexibility of nest preference observed at the colony level in experiment III.2 can be achieved under these assumptions. The first stage ('*Pre-emigration phase')* describes exploration and commitment behaviour prior to emigration; it is directly derived from the 'acceptance threshold model' developed by Robinson et al. (Robinson *et al.* submitted). The second stage ('*Emigration phase')* describes the commitment behaviour of scouts during emigration. It is inspired by an existing model of opinion formation with recruitment (de la Lama *et al.* 2006; de la Lama *et al.* 2007; Revelli *et al.* 2009).

Pre-emigration phase (Stage 1)

We used a Markov-chain model to describe the commitment behaviour of ants to their old nest and to the familiar site during the exploration period in the context presented in experiment III.2 (see Appendix for details, p48). We assumed that no recruitment occurs at that time. Ants can be either committed to a site or searching for a new site. Ants committed to either site can spontaneously abandon their commitment and start searching again. Ants discover nest sites independently, then assess their quality and compare it with an internal

threshold, committing to them or rejecting them accordingly (Figure III.2 A; see Robinson *et al.* submitted; Robinson *et al.* 2009b). As described in the Appendix (p48), this Markov-chain model rapidly converges to a limiting distribution of ants committed either to their old nest or to the familiar nest. It is therefore possible to calculate the average proportion of scouts committed to the familiar site at the end of exploration, i.e. at the onset of emigration ('*pre-committed scouts*'), as a function of the relative quality of the old nest and the familiar site.

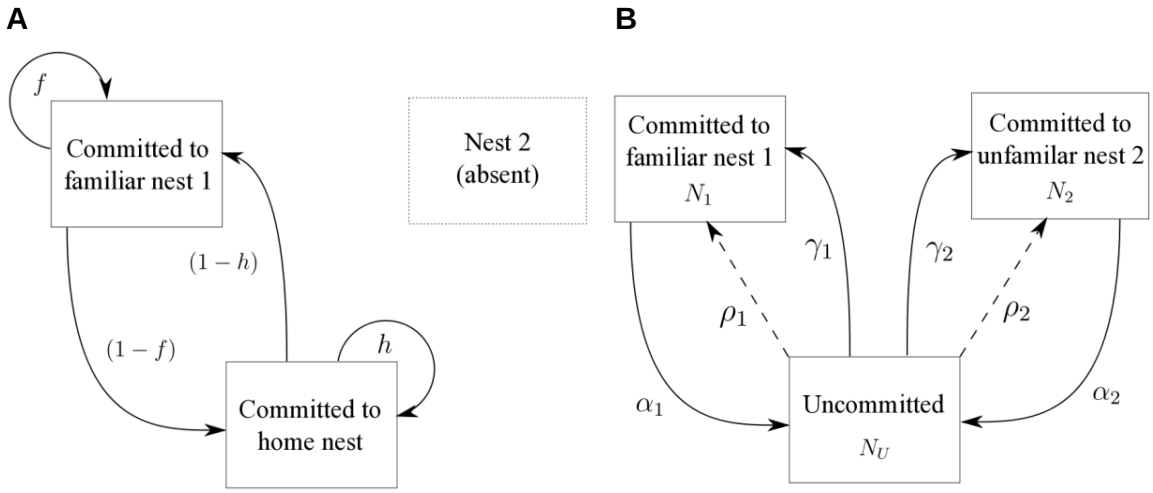

Figure III.2 State transition diagrams
(A) Pre-emigration phase (Stage 1) and **(B)** emigration phase (Stage 2). Solid lines indicate spontaneous transitions, dashed lines indicate recruitment.

Emigration phase (Stage 2)

We used a stochastic opinion formation approach to model expected nest choice in emigrations as a function of the relative quality of the alternatives and the proportion of scouts pre-committed to the familiar site (Figure III.2 B; see Appendix for details, p48). We specifically investigated whether this new model can reproduce the results observed in experiment III.2 (choice between one familiar and one unfamiliar, otherwise identical, mediocre nest sites). Because colonies develop an aversion towards familiar, mediocre nest sites, we assumed the overall perceived quality of the familiar site to be lower than that of the unfamiliar site. This aversion may, however, be partly countered by a small number of pre-committed scouts, which we assumed to remain permanently committed to the familiar nest during emigration. We used the results of the pre-emigration phase as input for the emigration phase to investigate how the relative quality of the old and familiar nest sites may influence nest choice at the colony level (see Appendix for details, p48).

RESULTS

Experiment III.1 – Aversion and nest choice accuracy

After 24 h, all naïve colonies (n = 20) confronted with a choice between a mediocre and a poor nest chose the mediocre nest (Figure III.3). This shows a very strong natural preference for the better alternative (binomial test: $p < 0.0001$). By contrast, informed colonies (n = 20), which were familiar with the mediocre, but not with the poor site prior to emigration, split their choice between the mediocre nest (n = 15) and the poor nest (n = 5; Figure III.3). Informed colonies therefore chose the poor nest significantly more often than naïve colonies (Fisher's test: $p = 0.047$), indicating that they had developed an aversion to the familiar, mediocre nest, which was strong enough to induce assessment errors in some colonies. Nevertheless, informed colonies still displayed a preference for the mediocre over the poor nest (binomial test: $p = 0.041$). Most colonies had therefore been able to overcome their aversion to the familiar nest and select the better option; however, the change in relative preference between the mediocre and the poor nest between both treatments reveals a form of collective irrationality.

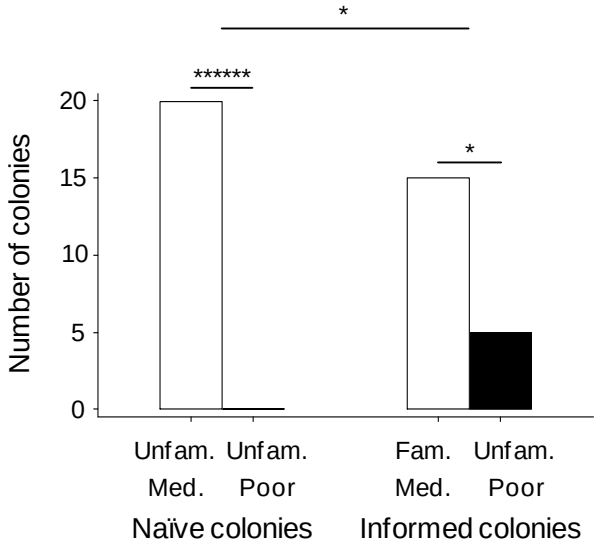

Figure III.3 Nest choice by naïve and informed colonies (experiment III.1)
Number of naïve (left) or informed (right) colonies choosing the mediocre (Med., white bars) or the poor nest (Poor, black bars) 24 hours after the onset of emigration, depending on the familiarity of each nest (Familiar: Fam., Unfamiliar: Unfam.). No colonies split. Binomial and Fisher's tests, *: $p < 0.05$; ******: $p < 0.0001$.

Experiment III.2 – Old nest quality and aversion intensity

Colonies housed in a good nest had developed an aversion towards the familiar, mediocre nest and preferred the unfamiliar option (Figure III.4; binomial test: $p < 0.005$), in agreement with the results of Franks et al. (2007). By contrast, colonies housed in a mediocre nest did not show any preference for either nest, but apparently chose randomly between them (Figure III.4; binomial test: $p = 0.19$). The difference in nest choice patterns for colonies housed in a good or in a mediocre nest was however marginally non-significant (Figure III.4; Fisher's exact test: $p = 0.075$). Aversion intensity at the colony level therefore appeared not to be determined by the absolute quality of the familiar nest only, but also by the quality of the colony's home nest.

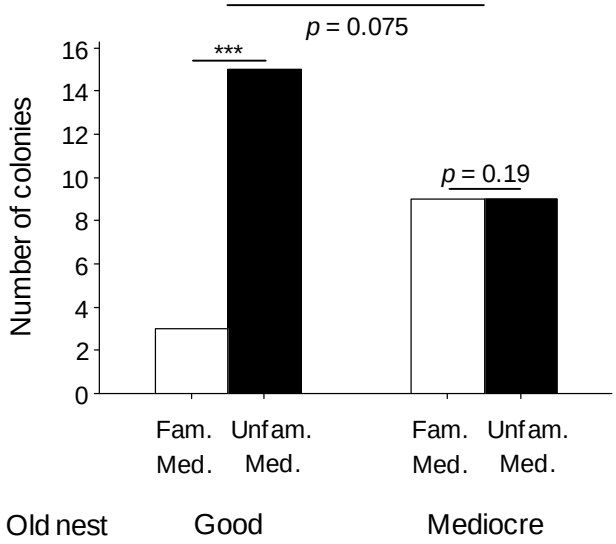

Figure III.4 Nest choice by colonies housed in good or mediocre nests (experiment III.2)
Number of colonies choosing the familiar (white bars) or unfamiliar (black bars) mediocre nest 24 hours after the onset of emigration, depending on the quality of their old nest. Binomial and Fisher's tests, ***: $p < 0.005$. Comparison of nest choice pattern between treatments used a two-tailed Fisher's exact test. Under each treatment, there were two split colonies (not shown).

Exploration intensity was higher for colonies housed in mediocre than in good nests: during exploration, colonies housed in mediocre nests had more workers inside the familiar nest (Figure III.5; GLMM: t = -4.567, df = 218, $p < 0.0001$) and higher traffic in and out of the familiar nest (Figure III.6; paired t-test, Entries: t = -2.55, df = 17, $p = 0.021$; Exits: t = -3.08, df = 17, $p < 0.01$). This result indicates that evaluation of the current nest promotes or inhibits search for better alternatives.

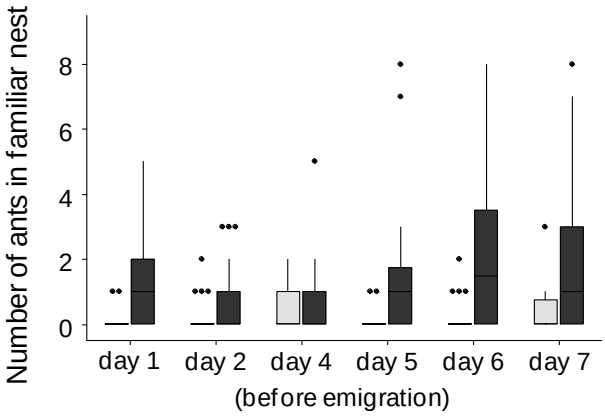

Figure III.5 Number of workers in the familiar nest during exploration (experiment III.2)
Interquartile range (rectangle), median (horizontal line), 1.5 x interquartile range (vertical whiskers) and outliers (solid circles) are presented for colonies with a good (light grey, n = 20) or mediocre (dark grey, n = 20) old nest. All colonies were scanned daily at 14h00. GLMM analysis identified three factors significantly influencing the number of workers in the familiar nest: quality of the old nest (t = -4.567, df = 218, $p < 0.0001$); colony size (t = -2.575, df = 18, $p = 0.019$) and time of observation (t = -2.859, df = 218, $p < 0.005$).

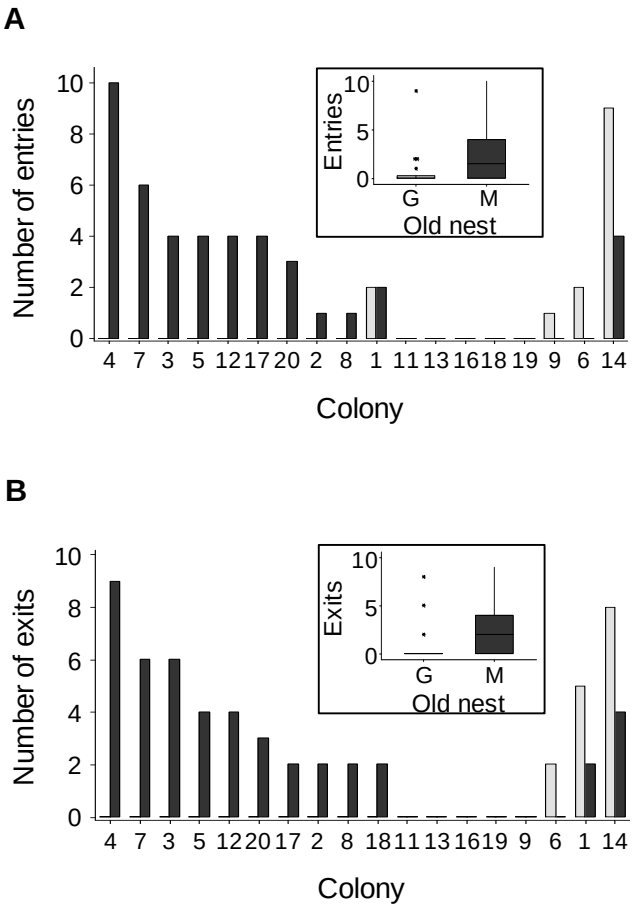

Figure III.6 Traffic in and out of the familiar nest during exploration (experiment III.2)
Number of workers entering **(A)** or leaving **(B)** the familiar nest during a single one-hour observation bout for colonies with a good (light grey) or mediocre (dark grey) old nest. Inserts show the same data pooled for all colonies: interquartile range (rectangle), median (horizontal line), 1.5 x interquartile range (vertical whiskers) and outliers (solid circles) are presented for colonies with a good (light grey, n = 18) or mediocre (dark grey, n = 18) old nest (paired t-test: Entries, t = -2.55, df = 17, $p < 0.05$; Exits, t = -3.08, df = 17, $p < 0.01$). The number of entries and exits was highly correlated for each colony under both treatments (Pearson correlation coefficient r = 0.935, n = 18, $p < 0.001$).

Modelling

The first stage of the model assumes that the proportion of scouts abandoning their commitment to their home nest and searching for alternative sites should increase when the quality of the home nest decreases; the number of scouts inspecting available nest sites should therefore increase as home nest quality decreases. Additionally, Stage 1 predicted that the proportion of scouts that commit to a familiar site should increase when the relative quality of the home nest decreases (see Appendix, p48). These predictions are in agreement with our data (experiment III.2) showing both increased traffic (Figure III.6) and residence (Figure III.5) in the familiar site when the home nest is of lower quality.

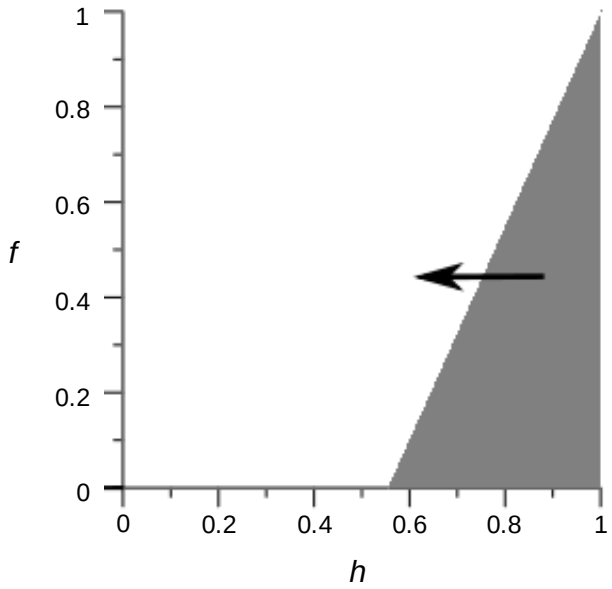

Figure III.7 Predictions from combined pre-emigration and emigration phases
The shaded region indicates the values of *h* and *f* in the pre-emigration phase (per visit acceptance probabilities of the old – or 'home' – nest and familiar site respectively, determined by their perceived qualities) in which the unfamiliar site is more likely to be chosen. In the unshaded region the familiar site is more likely to be chosen. Along the line dividing the regions the colony choice will be random. See Appendix for details.

The combined predictions from the two-stage model on nest choice are shown in Figure III.7: when the quality of the old nest was high during exploration, the unfamiliar site is more likely to be chosen during emigration (shaded region). Reducing the quality of the old nest relative to the familiar site (as indicated by the arrow) results in a decrease in the probability of choosing the unfamiliar nest, such that nest choice progressively becomes random (border line) then biased towards the familiar site (unshaded region), as the proportion of pre-committed scouts increases. This scenario is in agreement with the results observed in experiment III.2: for a fixed (mediocre) quality of the familiar site, colonies with a good old nest indeed preferred the unfamiliar site whereas colonies with a mediocre old nest chose randomly between familiar and unfamiliar sites (Figure III.4).

Results from Stage 2 also indicate that the proportion of pre-committed scouts required for random colony choice is usually quite small, with a maximum possible value of approximately 30% (see Appendix, p48).

DISCUSSION

Colonies of *T. albipennis* can collect information about available nest sites while their nest is still intact, and use this information in later emigrations (see Franks *et al.* 2007b and Chapter II). Here, we present two cases where this process induces modifications in nest preference depending on previous conditions. In experiment III.1, colonies which had familiarised themselves with a mediocre nest site prior to emigration chose differently from naïve colonies. Developing an aversion towards the familiar, mediocre nest site indeed led some colonies to later choose the poorer, unfamiliar option. By contrast, when given a choice between the same nests, naïve colonies were all able to select the better alternative. In experiment III.2, colonies which had familiarised themselves with a mediocre nest site prior to emigration chose differently depending on the quality of their old, home nest. Colonies housed in a good nest developed an aversion towards the familiar nest and later showed a strong preference for an otherwise identical, but unfamiliar nest. By contrast, colonies housed in a mediocre nest did not appear to develop any aversion towards the familiar, mediocre nest and later chose randomly between both nests. Previous experience has already been shown to affect emigration dynamics in *Temnothorax* ants (Healey & Pratt 2008; Langridge *et al.* 2004); our results indicate that it can also affect nest choice at the colony level.

That colonies changed their relative preference between two nest sites depending on previous conditions, although the absolute fitness-related values of these sites did not change, can be seen as a form of irrationality (Bateson & Healy 2005; Houston *et al.* 2007; Schuck-Paim *et al.* 2004; Waite 2001). Our results therefore appear to contrast with those of Edwards and Pratt (2009), who did not find evidence for irrational decisions in colonies of the related species *Temnothorax curvispinosus*. However, in that study, the authors tested for a specific form of rationality – independence from irrelevant alternatives – by varying the local context: specifically, they investigated whether the presence of a decoy nest affected the level of preference between two other nests, all nests being unknown at the time of emigration. By contrast, the apparent irrationality observed in our study was induced by variations in the background context, i.e. differences in experience with one of the two alternatives (experiment III.1) or differences in the previously experienced home nest quality (experiment III.2).

Apparent deviations from rationality have been suggested sometimes to reflect adaptive adjustments to local conditions or to occur as a side-effect of decision heuristics that usually perform well (Houston et al. 2007). Here, the seemingly irrational decisions observed in our experiments may similarly reflect a process allowing ant colonies to adjust their preference criteria to the experienced environment. The use of previous experience has been shown to allow solitary animals to make flexible choices and adjust their acceptance and/or preference criteria to the local quality distribution of potential food sources (Greggers & Menzel 1993; Hodges 1981), habitats (Davis 2007; Davis & Stamps 2004; Stamps & Davis 2006) or mates (Bakker & Milinski 1991; Collins *et al.* 2006; Collins 1995; Dukas 2005; Reid & Stamps 1997; Wagner *et al.* 2001). Similarly, the use of previously obtained information by ant colonies may confer them with greater flexibility in emigrations. Colony-level aversion strength towards a familiar nest site indeed did not depend on the absolute quality of that site, but rather on its quality relative to the home nest (experiment III.2). This should allow colonies to adjust to the local quality of available nest sites. Colonies are able to move to better sites when their own nest is still intact ('move to improve'; see Dornhaus *et al.* 2004), so a well-established colony is likely to occupy one of the best available nest sites in its surroundings. Developing an aversion towards sites of similar quality to that of the current nest – irrespective of their absolute quality – would therefore be detrimental, because it is unlikely that a much better site will suddenly become available and aversion would merely delay emigration. By contrast, developing an aversion towards sites of lower quality can be beneficial, as it should allow colonies to focus their search for better alternatives (Franks *et al.* 2007b). The quality of the home nest may therefore serve as an indicator to build reasonable expectations of the quality of future nests, and the optimal behaviour (e.g. developing an aversion towards a given available site or not) may differ depending on these expectations. In that case, the ants' change in acceptance criteria according to old nest quality cannot be considered as irrational, but as an adaptive adjustment to local conditions.

Natural selection is thought to shape 'rules of thumb' or decision heuristics which perform well in the environment in which they evolved, although they may induce occasional mistakes or perform badly in novel contexts (Gigerenzer *et al.* 1999; Houston *et al.* 2007). In experiment III.1, the apparent 'mistakes' observed (i.e. informed colonies choosing the poorer site) could similarly be a by-product of decision mechanisms allowing previous (aversion towards a familiar site) and current information (difference in quality between alternatives) to be combined, which is usually beneficial for colonies (see Franks *et al.* 2007b and Chapter II). Experiment III.1 stages a 'worst-case scenario' in which these two sources of information exerted opposite influences on nest choice: amplificatory recruitment processes should favour higher quality nests (i.e. the mediocre nest in this case), whereas aversion to a familiar site is likely to (i) induce slower population growth in that nest, because

scouts avoid it or are influenced negatively in their assessment, and (ii) redirect search towards other alternatives, indirectly resulting in faster population growth in alternative sites (i.e. the poor nest in this case). This conflict is likely to delay decision-making, and it is uncertain which nest will reach the quorum threshold first. In our experimental conditions, although a significant number of colonies chose the poorer option, site quality appeared to have a stronger influence than previous experience, as most colonies selected the better option. The decision mechanisms therefore appear to be self-correcting, which reduces the risk of errors when previous experience is misleading. It is therefore likely that the apparent mistakes observed in experiment III.1 are relatively infrequent in natural conditions.

Our results show that *T. albipennis* colonies are influenced by the quality of their home nest when assessing the suitability of an available nest site. How is this achieved? The literature on mate choice by solitary animals suggests several possible mechanisms by which individuals can take into account the quality of previously encountered options when assessing a new candidate: individuals can directly compare potential mates, or use an acceptance threshold which they adjust through pre-assessment of local mate quality or step-by-step updating after each encounter (see e.g. Bakker & Milinski 1991; Collins *et al.* 2006; Collins 1995; Reid & Stamps 1997). One could hypothesise that the flexibility in assessment criteria observed at the colony level in ants directly reflects similar flexibility at the individual level. For example, workers could memorise the quality of their current nest and compare it to the quality of encountered available sites, developing an aversion only towards sites of lower quality (*comparison strategy*). Comparisons by individual workers have indeed been suggested many times in empirical and theoretical studies, and until recently were supposed to play an important role in the decision process (Dornhaus *et al.* 2004; Mallon *et al.* 2001; Marshall *et al.* 2006; Pratt & Sumpter 2006; Pratt *et al.* 2005). However, recent studies have questioned the existence of individual comparisons and suggested that apparent comparisons at the collective level could merely derive from individual decision rules based on absolute evaluation of nest sites and fixed acceptance thresholds (Robinson *et al.* submitted; Robinson *et al.* 2009b). It is possible that these thresholds are adjusted through prolonged experience with the current nest's quality (*adjusted-threshold strategy*), so that ants housed in lower quality nests would have lower standards than ants housed in higher quality nests, which would explain the results from experiment III.2.

Here, we investigated a third, previously unconsidered scenario, related to the following question: can flexible, experience-dependent decisions at the colony level derive from fixed-threshold decision rules at the individual level (*fixed-threshold strategy*)? By combining a fixed acceptance threshold model of pre-emigration commitment (Stage 1) with a stochastic decision-making emigration model (Stage 2), we show that fixed thresholds in

individuals can produce flexible collective choices. This is because the quality of the home nest determines the proportion of ants that are dissatisfied with it and search for alternative sites, which in turn influences future decisions at the colony level. Additionally, fixed thresholds in individuals can also result in variable aversion strength towards a given site if there is intra-colony variation in acceptance thresholds. Indeed, in that case different subsets of workers are involved in searching and assessing nest sites depending on the context. For example, for colonies housed in a good nest, only workers with a relatively high acceptance threshold will leave the nest and look for alternatives. Most of these workers should therefore reject the familiar, mediocre site when they visit it because its quality falls well below their acceptance threshold. This results in strong aversion towards that site at the colony level. By contrast, for colonies housed in a mediocre nest, exploring workers will have a greater range of thresholds, and those with lower thresholds can be expected to commit to the familiar, mediocre site, whereas those with higher thresholds should reject it. In this case, as shown by our analytical results, the influence of these two categories of workers can cancel out for biologically plausible parameters (see Appendix, p48), resulting in the observed absence of aversion to the familiar nest at the colony level. One prediction of this scenario is that exploration intensity will depend on the absolute quality of the home nest: if workers use a fixed-threshold rule to decide whether to leave their nest and look for better alternatives, then exploration intensity should be higher for colonies housed in lower quality nests. Our observations are in agreement with these predictions (Figure III.5; Figure III.6), although our results do not at present allow us definitively to select or rule out any of the three scenarios presented above (comparison, adjusted-thresholds or fixed-thresholds).

Irrationality is usually considered as evidence for comparative evaluation mechanisms at the individual level (Bateson & Healy 2005; Waite 2001). Here, we have observed seemingly irrational decisions at the colony level induced by the background context. (i.e. decisions where the relative preference between options depends strongly on previous experience). This may be indicative of a comparative strategy at the colony level. Interestingly, however, our analytical results demonstrate that apparent comparative evaluation at the colony level does not necessarily rely on comparative evaluation in individuals, but may simply emerge from individuals using absolute evaluation coupled with threshold-based decision rules. Strikingly, the same individual-level decision strategy has previously been suggested to protect colonies from irrationality induced by the local context (i.e. decisions where the relative preference between options depends strongly on the composition of the choice set; see Edwards & Pratt 2009; Robinson *et al.* submitted). This simple individual rule has therefore the potential to allow colonies to both make relatively robust decisions based on current information and adjust their acceptance criteria to local conditions according to previous information. This is a new illustration of the principle that

complex collective properties can emerge from the interaction of simpler units (see e.g. Camazine *et al.* 2001). We hope our results will stimulate new experimental and analytical studies investigating how individual decision-making strategies relate to apparent collective strategies, and how previous experience can influence decision-making in animal groups without necessarily requiring experience-dependent changes in individuals.

In the first two Chapters, we have examined how prior familiarisation with good and/or mediocre available nest sites affects the collective performance of colonies in later emigrations. The second part of this thesis will aim at investigating the underlying mechanisms allowing colonies collectively to exploit information previously gathered by individuals.

APPENDIX

Pre-emigration phase (Stage 1)

We modelled ants as independently discovering nest sites, assessing their quality (with noise) and comparing it with an internal threshold, then accepting or rejecting them accordingly. We made two modifications as follows: Robinson et al. (submitted) modelled site acceptance during emigration and considered that once scouts accept a site, they remain committed to it until the end of emigration and may start recruiting. In the pre-emigration period, however, we considered that committed scouts do not recruit, but may subsequently abandon their commitment and assess other sites.

We modelled this as a discrete-time Markov-process whose state transitions are shown in Figure III.2 A (see Appendix I, p159 for details). We assumed that probability *h* of accepting the old (or 'home') nest is greater than probability *f* of accepting the familiar site. This can occur for several reasons: the old nest can be of physically higher quality, or merely perceived as better due to the presence of nestmates, brood and the queen. Additionally, even if old and familiar sites are of the same perceived quality, if we assume a distribution of acceptance thresholds in the colony, then those scouts dissatisfied with the old nest and discovering the familiar site will have a higher average threshold than those scouts staying in the old nest, leading to a correspondingly lower probability of accepting the familiar site.

The model outlined above predicts the pattern seen in the experimental data of higher entrance and exit rates at the familiar site when the home site is of lower quality (Figure III.6; see Appendix I, p159 for details). Additionally, it converges to a limiting distribution over its states, which predicts the increased residence observed in the familiar site when the quality of the old nest is lower (Figure III.5; see Appendix I, p159 for details).

The limiting distribution of the model can be used to calculate the average proportion of scouts committed to the familiar site when emigration is induced, for given relative site qualities. This proportion increases when the quality of the old nest relative to the familiar nest decreases and can be used as an input parameter for the stochastic decision-making model described below (see Appendix I, p159 for details).

Emigration phase (Stage 2)

To model nest choice by emigrating colonies, we applied an existing stochastic model of opinion formation with recruitment by de la Lama *et al.* (2006, 2007). The states and transitions in this continuous-time model are depicted in Figure III.2 B: ants may either be committed to the familiar nest (N_1), committed to the unfamiliar nest (N_2) or uncommitted to

either nest (N_U). Uncommitted ants may spontaneously discover and commit to either nest, or be actively recruited by committed ants and commit to either nest. Committed ants may also spontaneously abandon their commitment and become uncommitted. These six rates may in general be independent.

We further assume that the pre-committed scouts from the pre-emigration commitment model (ϕ) remain permanently committed to the familiar nest during the decision making process (Revelli *et al.* 2009). These ants may not spontaneously abandon their commitment to the familiar nest, but crucially may recruit uncommitted ants to become committed to nest 1. These pre-committed ants may partly counter the aversion to the familiar nest, depending on their proportion among total scouts, which itself depends on the relative qualities of the old and familiar nests.

This model begins with a microscopic, continuous-time master equation description of the transitions. From this the macroscopic equations for the proportion of the colony in each state, as well as the fluctuations about these, may be derived. These results are then used to calculate the conditions for which we may expect equal probabilities that the majority of scouts are committed to either nest as a function of the parameters of the model, in particular the proportion of pre-committed scouts ϕ. As ϕ is a function of the nest-quality parameters h and f in the pre-emigration model, we can find, under certain generalised assumptions, the values of h and f required for random nest choice, as depicted in Figure III.7 (see Appendix I, p159 for details).

Figure III.7 may help explain the results observed in experiment III.2 (Figure III.4): reducing the quality of the home site for a fixed quality of familiar nest results in an increased proportion of pre-committed scouts, which counter the effect of aversion to the familiar nest. If the old home nest is good and the familiar site is mediocre (experiment III.2, treatment 2), the system will be in the shaded area of Figure III.7, i.e. greater chance of choosing the unfamiliar than the familiar site. This indicates that pre-committed scouts are not enough to compensate the effect of aversion to the familiar site. Keeping the quality of the familiar site constant, reducing the perceived quality of the old nest will move the system parallel to the horizontal axis as indicated by the arrow. This will reduce the chances of the unfamiliar site being chosen, passing through random nest choice (line), as the proportion of pre-committed scouts increases (experiment III.2, treatment 1). Finally, low enough old nest quality should result in a greater chance of choosing the familiar than the unfamiliar nest, as pre-committed scouts are sufficiently numerous and influential to overcome the effects of aversion.

PART II – UNDERLYING MECHANISMS OF INFORMATION USE IN ANT EMIGRATIONS TO FAMILIAR NEST SITES

Chapter IV. The Roles of Private and Social Information in Ant Emigrations to Familiar Nest Sites

ABSTRACT

When making a decision, gregarious animals can rely on two potential sources of information: private information (gathered independently by individuals), and social information (acquired through eavesdropping or communication). The use of social information is particularly relevant for large animal groups making collective decisions through self-organised, distributed mechanisms. Individuals in such groups are usually assumed to be identical and to follow the same set of rules. However, there is increasing evidence in vertebrates that certain key individuals possessing highly pertinent, private information might be particularly influential on the group's choices and may play the role of effective leaders. Here, we investigate the relative roles of private and social mechanisms in the collective exploitation of information about available nest sites gathered previously by exploring individuals in the house-hunting ant *Temnothorax albipennis*. In particular, we examine whether well-informed individuals might play a key role in orienting emigrations towards high-quality, familiar nest sites by using private information. We show that experienced workers possess private information about the location of such familiar nests, which allows them to find these nests faster than through random exploration. This is of particular importance because it brings forward the following stages of emigration, thus favouring familiar over novel nest sites. Information is then transferred socially between informed and naïve workers, allowing all scouts to expedite decisions about familiar nest sites. It therefore appears that the collective exploitation of prior information in emigrating colonies of *T. albipennis* involves an interplay between private and social information.

INTRODUCTION

Animals constantly have to make crucial decisions affecting their fitness, e.g. while foraging or while selecting a mate or a habitat. To discriminate and to choose accurately between several alternatives, animals need to gather information so as to reduce uncertainty over the different options. Although solitary animals have to rely mostly on information gathered personally (i.e. private information), group-living animals have access to two different sources of information: private information and social information, provided by conspecifics (Giraldeau *et al.* 2002; Grüter *et al.* 2008; Grüter *et al.* 2010; Kerth *et al.* 2006; King & Cowlishaw 2007). Social information may be communicated voluntarily (Earley 2010; Fewell 2003; O'Donnell & Bulova 2007) or may consist of easily accessible, public information acquired by eavesdropping on the performance of conspecifics or copying their behavioural decisions (Valone 2007; Valone & Templeton 2002).

Socially acquired information is usually considered beneficial because it confers many advantages, such as – among others – reducing the costs associated with private

information gathering (Galef & Giraldeau 2001; Giraldeau & Caraco 2000; O'Donnell & Bulova 2007; Wikelski *et al.* 2001) and allowing faster acquisition of information (Clark & Mangel 1986); increasing the range of perception and accessing higher-order computational capacities (Couzin 2007; Krause *et al.* 2010; O'Donnell & Bulova 2007); increasing the accuracy of decisions, especially in large groups (King & Cowlishaw 2007; List 2004; Simons 2004; Sumpter *et al.* 2008b; Surowiecki 2004); and decreasing the sensitivity to local noise and random environmental fluctuations (Clark & Mangel 1984; Couzin 2007). However, recent studies have rightly pointed out that socially acquired information can also incur substantial costs in certain situations. For example, waiting for social information rather than gathering private information may reduce efficiency in resource exploitation (Dechaume-Moncharmont *et al.* 2005), or lead to a decrease in the overall reliability of information, therefore reducing the ability of groups to make correct decisions (Giraldeau *et al.* 2002; King & Cowlishaw 2007). Additionally, the use of social information can occasionally lead to erroneous informational cascades by amplifying individual mistakes (Giraldeau *et al.* 2002; Laland & Williams 1998). The degree to which individuals rely on their private vs. social information may therefore depend on various factors, such as group size (Anderson & McShea 2001; Aron *et al.* 1988; King & Cowlishaw 2007; O'Donnell & Bulova 2007), reliability of private information (King & Cowlishaw 2007; van Bergen *et al.* 2004), environmental heterogeneity (Boulinier & Danchin 1997; Couzin 2007) and resource availability (Dechaume-Moncharmont *et al.* 2005).

Evidence for the role of socially acquired information in decision-making has been reported both in gregarious species (Valone 2007; Valone & Templeton 2002; e.g. in habitat selection: Danchin *et al.* 2001; Doligez *et al.* 2004; Parejo *et al.* 2007; Part & Doligez 2003; Redmond *et al.* 2009; Reed *et al.* 1999; Ward 2005; foraging: Galef & Giraldeau 2001; Giraldeau 1997; opponent assessment: Freeman 1987; Johnsson & Akerman 1998; Oliveira *et al.* 1998; Peake & McGregor 2004; mate choice: Dugatkin 1996; Galef & White 2000; Gibson & Hoglund 1992; Mennill *et al.* 2002; Nordell & Valone 1998; navigation in group travelling animals: Couzin *et al.* 2005; Sumpter 2006) and in highly cooperative animal societies, such as eusocial insects (Anderson & Ratnieks 1999; Fewell 2003; Hölldobler & Wilson 1990; O'Donnell & Bulova 2007). The use of social information is particularly developed in these societies because natural selection has favoured active communication between group members to ensure effective sharing of information and successful cooperative interactions (see e.g. Anderson & Ratnieks 1999; Dornhaus *et al.* 2006; Fewell 2003; Leadbeater & Chittka 2007; O'Donnell & Bulova 2007).

In insect societies, collective processes are usually thought to be self-organised, i.e. to emerge from local interactions between similar individuals following simple behavioural

rules of thumb in response to local information – both private and social (Bonabeau *et al.* 1997; Camazine *et al.* 2001; Sumpter 2006; Visscher 2007). However, individuals are not all identical and certain individuals can play a key role in the organisation of collective processes. For example, highly specialised or active individuals can have a strong influence on task performance in ant colonies (Dornhaus *et al.* 2008; Robson & Traniello 1999; Sendova-Franks *et al.* 2010). Individuals can also vary in their access to information. For example, workers performing or specialising on specific tasks may have more and/or higher quality information than other classes of workers (Anderson & Ratnieks 1999; Gordon 2002; Jackson *et al.* 2006). Additionally, experienced individuals may possess specific, private information which influences their behaviour more than social information does (Aron *et al.* 1993; Aron *et al.* 1988; Grüter *et al.* 2008; Grüter *et al.* 2010). Such well-informed individuals could play a key role in the transfer of information through the colony and the regulation of division of labour (Anderson & Ratnieks 1999; Fewell 2003; O'Donnell & Bulova 2007).

Self-organised collective decision-making process can be strongly influenced by a few well-informed, key individuals, or 'leaders'. This has been especially well studied in the context of collective movements in vertebrates, including humans (Couzin *et al.* 2005; Dyer *et al.* 2008; Dyer *et al.* 2009; Faria *et al.* 2010b; Lusseau & Conradt 2009; Sumpter *et al.* 2008a; Sumpter 2006), but has received far less attention in collective decision-making by insect colonies. This chapter presents data on the key role of well-informed individuals in nest site selection by emigrating *T. albipennis* colonies.

In previous chapters, it was shown that *T. albipennis* colonies gather valuable information about available nest sites prior to emigration, then retrieve and use it later when their nest is damaged, thus improving colony performance in emigrations. Information about suitable sites is primarily gathered by a minority of workers (i.e. scouts that discover and explore the sites), and potentially stored under two, non-exclusive forms: it could be stored in a common repository of information, e.g. by laying pheromones leading to or inside the nest site (social information), or remain private, i.e. stored in the memory of informed workers and/or individual-specific chemical marking, frequently used by *Temnothorax* ants (Aron *et al.* 1988; Mallon & Franks 2000; Maschwitz *et al.* 1986; Mugford *et al.* 2001). In the latter case, informed individuals would play a key role in retrieving information about suitable nest sites during emigrations. In this chapter, the relative role of informed vs. naïve individuals is thus investigated in the context of emigrations to high-quality, familiar and unfamiliar nest sites.

METHODS

Experimental design

All workers in 10 colonies of *T. albipennis* (colony size: range 112-230, median 162.5 workers) were individually marked with unique combinations of coloured paint dots to allow individual identification, as described in Sendova-Franks & Franks (1993).

Experiments were carried out in the geometrically complex arenas described in Chapter II (Figure II.1, see p15). Colonies housed in good nests (see p14) were positioned in the middle of the central dish and allowed to explore the experimental arena for one week. Throughout exploration, all colonies could freely visit an available, good nest site (familiar site) identical to their home nest, positioned at one end of the arena. They were then induced to emigrate and *choose between the familiar site and an identical, unfamiliar nest site* introduced at the other end of the arena at the onset of emigration.

Data recording and analysis

Two webcams connected to motion detector software were used to monitor all activity through the entrance of the new nests during emigrations, as explained in Chapter II (see p17). Both webcams were already present during the entire exploration period, and allowed the monitoring of all activity in and out of the familiar nest during exploration.

Analysis of exploration pictures allowed the identification of all workers that entered the familiar site during exploration week, and therefore potentially had private information about that site ('Informed workers'). All other workers (i.e. those which did not visit the familiar site during exploration) were considered as 'Naïve'. Entrance and exit times were recorded for the whole duration of exploration, so that the total number of visits and their duration could be calculated for every informed worker. A total of 7311 visits (range: 46-1149, median 723.5 per colony) were thus analysed. Because workers occasionally walked through the nest entrance upside down and because some workers lost their paint marks, it was sometimes impossible to assign a certain event (i.e. an entrance or exit) to a given worker. The percentage of assigned events was however high for all colonies (median 98.4%; range 93.6-100%).

In emigrations, discovery and assessment times were recorded for both new nest sites. Additionally, colony distribution was evaluated at the end of emigration by counting the total number of items (brood plus adults) inside each new nest site and calculating the proportion of items observed in the familiar site, as explained in Chapter II (see p18).

Analysis of emigration pictures allowed the recording of all entrances, exits and recruitment acts (i.e. tandem running and carrying) for both new nest sites during emigrations. Analysis was carried on for each site until the nest population reached 20 workers, or until the end of emigration if that value was not reached. The nest population over time was determined using the accumulated number of entrances and exits since the beginning of emigration. A value of 20 was chosen because it is at the higher end of the quorum threshold range usually observed in *T. albipennis* (Dornhaus & Franks 2006; Franks *et al.* 2006a; Franks *et al.* 2003a; Pratt 2005; Pratt *et al.* 2002). Any decisions made by individuals after this value has been exceeded are therefore likely to derive from social interactions within the new site and not to reflect any differences in individual private information.

All workers participating in emigration to either new nest site were identified, and the time and nature of their first entrance in the nest (i.e. independent discovery, recruitment by tandem running or transport by a nestmate) were recorded. Additionally, all recruiters were identified and the time and nature of all recruitment acts (i.e. tandem run or transport) were recorded. All workers observed entering a nest site were considered as potential recruiters, except those that were carried to the site by nestmates.

Statistical analyses

Colony-level variables (i.e. discovery time, assessment time, number of tandem runs, time of tandem runs and time of transport) were compared among nests using SPSS general linear mixed model procedure (GLMM) with fixed factor ‘New nest site’ (familiar vs. Unfamiliar) and random factor ‘Colony’. Number of independent discoverers and individual independent discovery times were analysed with a GLMM procedure with fixed factors ‘New nest site’, ‘Information’ (informed vs. Naïve) and their interaction, and random factor ‘Colony’. Independent discovery times were then reanalysed with a more complete GLMM model including all preceding factors, plus the covariate ‘Number of visits’, ‘Total visit time’ or ‘Recency of last visit’ and their interaction with ‘New nest site’. Individual latencies to first tandem run were analysed with a GLMM procedure with fixed factors ‘New nest site’, ‘Information’ and their interaction, covariate ‘Time of first discovery’ and random factor ‘Colony’. Individual latencies to first transport were analysed with a GLMM procedure with fixed factors ‘New nest site’, ‘Information’, ‘First recruitment act’ (tandem run vs. transport) and interaction New nest site x Information, covariate ‘Time of first discovery’ and random factor ‘Colony’. We selected the model fitting our data best by using a stepwise backward procedure. Statistical significance was tested using an Analysis of Deviance with a Type III Sum of Squares method (comparison of the full model to the full model without the factor of interest). Normality and homoscedasticity of residuals were checked using Kolmogorov-

Smirnov and Levene's tests. If residuals were not normally distributed, we applied either log- or power-transformation to the data.

Colony distribution at the end of emigration (i.e. proportion of the colony in the familiar nest) could not be normalised using classical data transformation and was therefore tested using a one-sample Wilcoxon test with a null hypothesis of random choice (i.e. expected median of 0.5).

Individual propensity to lead tandem runs depending on information (informed vs. naïve) and on nest site (familiar vs. unfamiliar) was analysed overall by comparing the number of potential recruiters with the number of actual tandem leaders in each category using Pearson chi-squared test. Additionally, propensity to lead tandem runs was tested for each nest site by comparing the number of potential recruiters with the number of actual tandem leaders using Fisher's exact tests. Finally, the proportion of informed workers among all potential recruiters or among actual tandem leaders was compared between nests using Fisher's exact tests.

RESULTS

Nest visits

Analysis of all exploration visits (n = 7311; range 46-1149, median 723.5 per colony) allowed the identification of 281 informed workers in total (range 11-42, median 28.5 workers per colony, representing range 9.2-25.2%, median 16.8% of the colony's total workforce). Analysis of all emigration visits (n = 4710; familiar nest: range 82-525, median 301.5; unfamiliar nest: range 12-550, median 128.5 visits per colony) allowed the identification of a total of 875 workers involved in emigrations (familiar nest: range 21-82, median 63; unfamiliar nest: range 3-101, median 24.5 workers per colony).

Colony-level emigration data

Familiar nest sites were discovered significantly earlier than unfamiliar nest sites (Figure IV.1 A; GLMM, effect of nest site, $F_{1,9} = 9.351$, $p < 0.05$), but there were no significant differences in the assessment time of familiar vs. unfamiliar sites (Figure IV.1 A; GLMM, effect of nest site, $F_{1,8} = 0.559$, $p = 0.48$). At the end of emigration, colonies appeared to prefer familiar over unfamiliar nest sites, but this trend was not significant (5 colonies split and 5 chose the familiar nest; exact binomial test: $p = 0.062$; see Figure IV.1 B for data including split colonies; 1-sample Wilcoxon test with expected median of 0.5, n = 10, $p = 0.067$). This may be due to the lower sample size used in this experiment (n = 10) compared to the nest choice experiment presented in Chapter II (Figure II.3, see p22; n = 33), where similar, yet significant trends were observed.

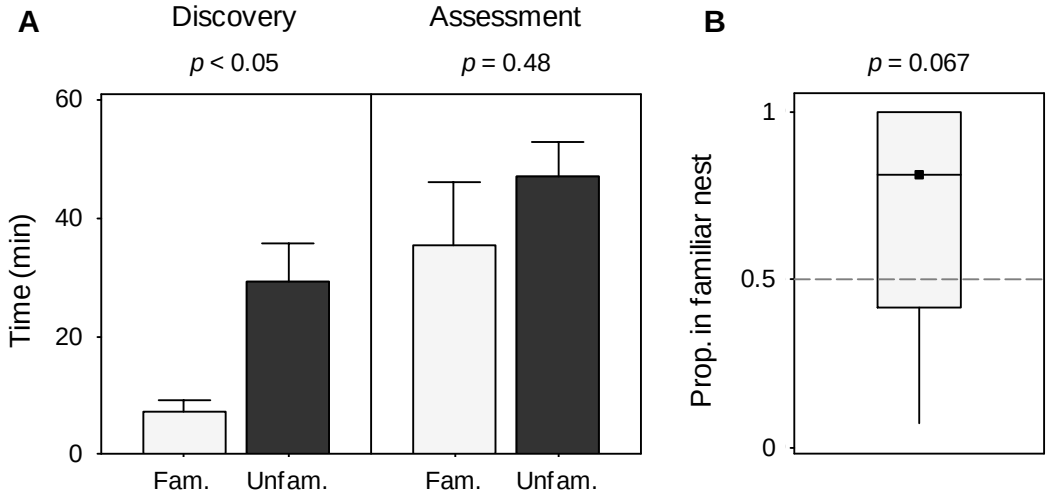

Figure IV.1 Colony-level emigration data
(A) Discovery and assessment times of familiar (light grey) and unfamiliar (dark grey) nest sites (n = 10). Bars and whiskers represent means and standard errors, respectively. *P*-values are given for the effect of nest site on both variables (GLMM; no data transformation). **(B)** Proportion of colony items observed in the familiar nest at the end of emigration (n = 10). Full squares, rectangles and whiskers represent the median, interquartile range, and full range, respectively. The broken line represents expectations under the hypothesis of random choice between both nests (one-sample Wilcoxon test).

Independent discoveries

During emigrations, naïve workers (i.e. workers which had not previously visited either nest site) were as likely independently to discover the familiar as the unfamiliar nest site (Figure IV.2 A; GLMM, LSD post-hoc test: $p = 0.36$) and took a similar amount of time to find both sites (Figure IV.2 B; GLMM, LSD post-hoc test: $p = 0.09$). This strongly suggests that naïve workers explored the arena randomly while searching for potential new nest sites.

By contrast, informed workers (i.e. workers which had visited the familiar nest during exploration) were significantly more likely independently to discover the familiar rather than the unfamiliar nest site (Figure IV.2 A; GLMM, LSD post-hoc test: $p = 0.04$) and took significantly less time to find the familiar than the unfamiliar site (Figure IV.2 B; GLMM, LSD post-hoc test: $p < 0.001$). Informed workers heading to the familiar site were also significantly faster in finding the nest than naïve workers (Figure IV.2 B; GLMM, LSD post-hoc tests, Informed/Familiar vs. Naïve/Familiar: $p < 0.001$; Informed/Familiar vs. Naïve/Unfamiliar: $p < 0.001$). Informed workers therefore had information about the location of the familiar nest site, allowing them to find that nest more efficiently than by random exploration. Because naïve workers were apparently unable to use that information, our results strongly suggest that information about the location of the familiar site was private.

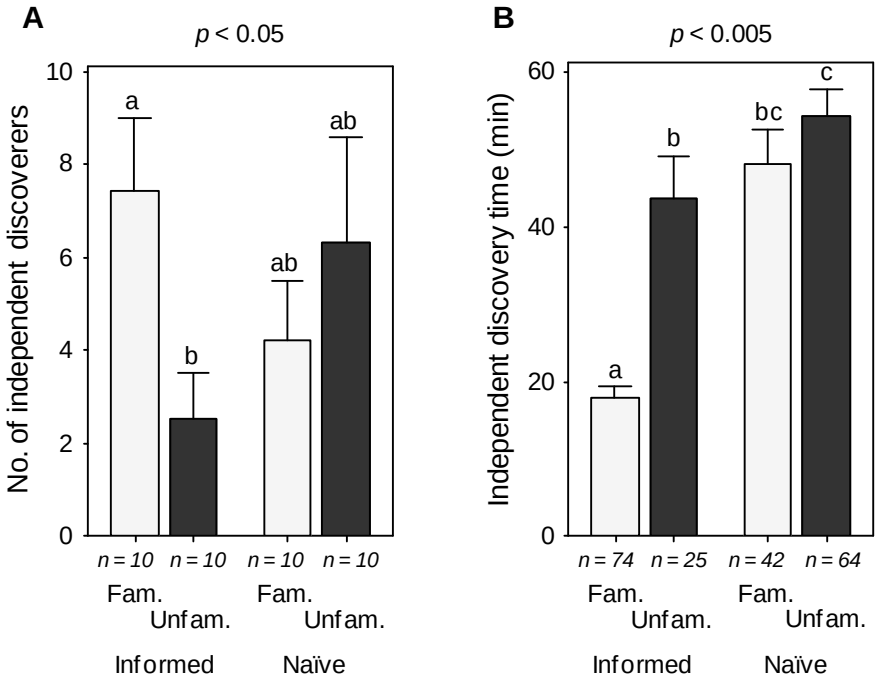

Figure IV.2 Independent discoveries
(A) Number of independent discoverers per colony, and **(B)** time of individual independent discoveries for familiar (Fam., light grey) and unfamiliar (Unfam., dark grey) nest sites. Data is shown for informed and naïve workers. Bars and whiskers represent means and standard errors, respectively. *P*-values are given for the effect of the interaction between nest site and information status on both variables (GLMM; independent discovery time was power-transformed). Same letters indicate no differences, whereas different letters indicate significant differences ($p < 0.05$) in LSD post-hoc tests.

The intensity of prior exploration activity (total number of visits and total time spent inside the familiar nest) and the recency of the last visit to the familiar site (i.e. time elapsed between the end of the last visit and the beginning of emigration) did not influence informed workers' likelihood of heading towards the familiar nest site (GLMM on the first nest discovered with binomial error structure: effects of total number of visits: X^2 = 0.14, df = 1, p = 0.71; total visit time: X^2 = 0.284, df = 1, p = 0.59; recency of last visit: X^2 = 0, df = 1, p = 1). There was no effect of these parameters on independent nest discovery times by informed workers (Figure IV.3; GLMM: effects of total number of visits: $F_{1,87}$ = 2.147, p = 0.15; total visit time: $F_{1,86}$ = 0.230, p = 0.63; recency of last visit: $F_{1,87}$ = 2.034, p = 0.16; interaction with nest: $F_{1,85}$ or $F_{1,86}$ < 1.1, p > 0.3 for all three variables). Familiar nest sites were discovered by informed workers earlier than unfamiliar nest sites independently of how much information these workers possessed about the familiar site (GLMM; effects of nest site: $F_{1,88}$ = 19.268, p < 0.001).

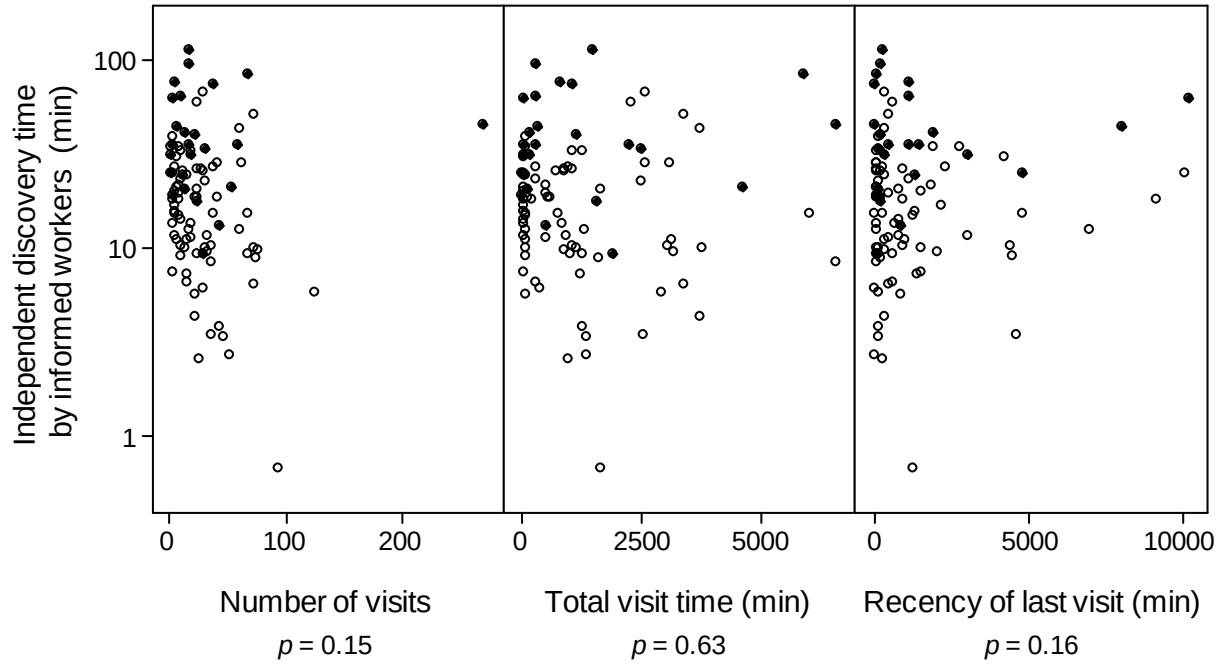

Figure IV.3 Level of information and independent discoveries by informed workers
Time of independent discoveries of familiar (open circles) and unfamiliar (full circles) nest sites by informed workers as a function of the total number of visits of the familiar site during exploration (left), the total time spent in the familiar site during exploration (middle), and the recency of the last visit to the familiar site (right). Each point represents an informed worker. *P*-values are given for the effect of number of visits, total visit time; and recency of last visit on independent discovery times, respectively (GLMM; discovery times were log-transformed).

Recruitment by tandem running

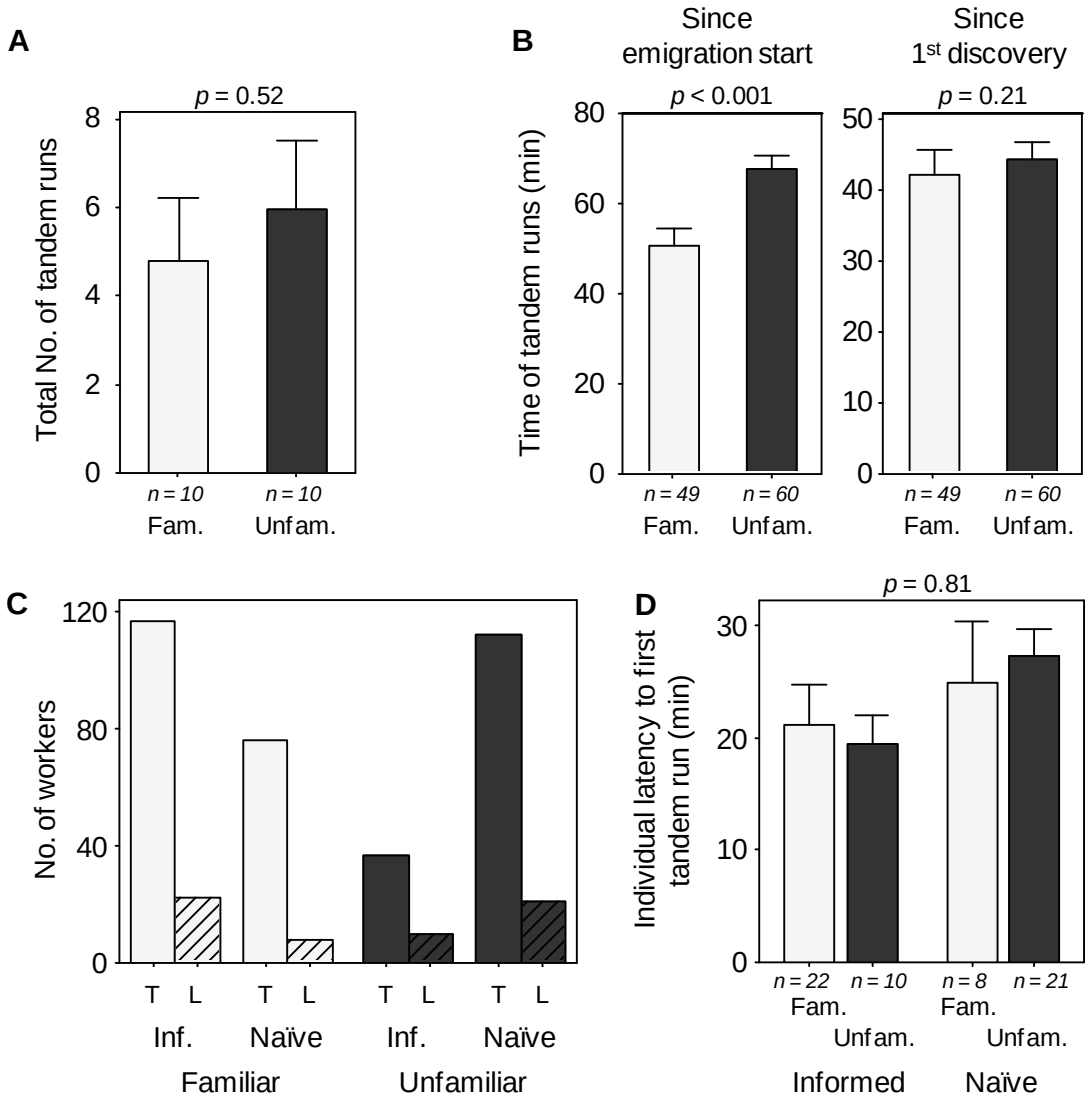

Figure IV.4 Recruitment by tandem running
(A) Total number of successful forward tandem runs to familiar (Fam., light grey) and unfamiliar (Unfam., dark grey) nest sites. **(B)** Tandem run times to familiar and unfamiliar nest sites since emigration start (left) or since first discovery of the site (right). Bars and whiskers represent means and standard errors, respectively. *P*-values are given for the effect of nest site (GLMM; no data transformation). **(C)** Total number of informed (Inf.) and naïve potential recruiters (T, open bars) and total number of informed and naïve tandem leaders (L, hashed bars) for familiar and unfamiliar nest sites (Pearson chi-squared test: $X^2 = 3.53$, df = 3, $p = 0.32$; Fisher's exact tests, familiar site: $p = 0.23$, unfamiliar site: $p = 0.38$; potential recruiters: $p < 0.001$, tandem leaders: $p < 0.005$. **(D)** Individual latencies to first tandem run to familiar and unfamiliar sites for informed and naïve tandem leaders. Bars and whiskers represent means and standard errors, respectively (GLMM, effects of interaction nest site x information: $F_{1,47} = 0.056$, $p = 0.81$; nest site: $F_{1,48} = 0.052$, $p = 0.82$; information: $F_{1,48} = 1.383$, $p = 0.25$; no data transformation).

Overall, similar numbers of tandem runs were led to the familiar and unfamiliar nest sites (Figure IV.4 A; GLMM, effect of nest site: $F_{1,9} = 0.460$, $p = 0.52$). Tandem running to familiar nest sites occurred earlier in the emigration than to unfamiliar sites (Figure IV.4 B;

GLMM on time of individual tandem runs since emigration start, effect of nest site: $F_{1,98}$ = 11.037, $p < 0.001$); however, this trend disappeared when taking into account the time of first discovery of the nest (Figure IV.4 B; GLMM on time of tandem runs since first discovery, effect of nest site: $F_{1,98} = 1.576$, $p = 0.21$). Any differences between nest sites in the timing of tandem runs could therefore be attributable to the earlier discovery of the familiar nest.

Informed workers had a greater share in tandem running to the familiar site than to the unfamiliar site (Figure IV.4 C; Fisher's exact test: $p < 0.005$). However, this was not due to informed workers being more likely to lead tandem runs to the familiar site, or less likely to lead tandem runs to the unfamiliar site, than naive workers (Figure IV.4 C; Pearson's Chi-squared test: $X^2 = 3.53$, df = 3, $p = 0.32$; Fisher's exact tests, familiar site: $p = 0.23$; unfamiliar site: $p = 0.38$), but simply to the higher proportion of informed scouts present, and therefore available to recruit, at the familiar nest site (Figure IV.4 C; Fisher's exact test: $p < 0.001$). Additionally, individual latencies to tandem running (i.e. time interval between the first entrance in the nest and the first tandem run led) were similar for informed and naïve tandem leaders at both nest sites (Figure IV.4 D; GLMM; effects of interaction nest site x information: $F_{1,47} = 0.056$, $p = 0.81$; nest site: $F_{1,48} = 0.052$, $p = 0.82$; information: $F_{1,48} = 1.383$, $p = 0.25$).

Transport

Transport started earlier towards familiar than unfamiliar nest sites (Figure IV.5 A; paired t-test, t = -2.307, df = 9, $p < 0.05$). This was partly due to the earlier discovery of the familiar sites. Additionally, both informed and naïve workers had lower individual latencies to first transport (i.e. time interval between the first entrance in the nest and the first transport act) at the familiar than at the unfamiliar nest site (Figure IV.5 B; GLMM on individual latencies to first transport, effect of nest site: $F_{1,100} = 4.996$, $p < 0.05$). Informed workers also tended to have lower latencies to first transport than naïve workers at the familiar site, but this trend was not significant (Figure IV.5 B; GLMM on individual latencies to first transport, effect of interaction nest site x information: $F_{1,98} = 1.608$, $p = 0.21$). The time of first entrance in the new nest and nature of the first recruitment act (i.e. tandem run or transport) also had a significant influence on individual latencies to first transport (GLMM, $F_{1,100} = 4.131$, $p < 0.05$ and $F_{1,100} = 21.277$, $p < 0.001$, respectively).

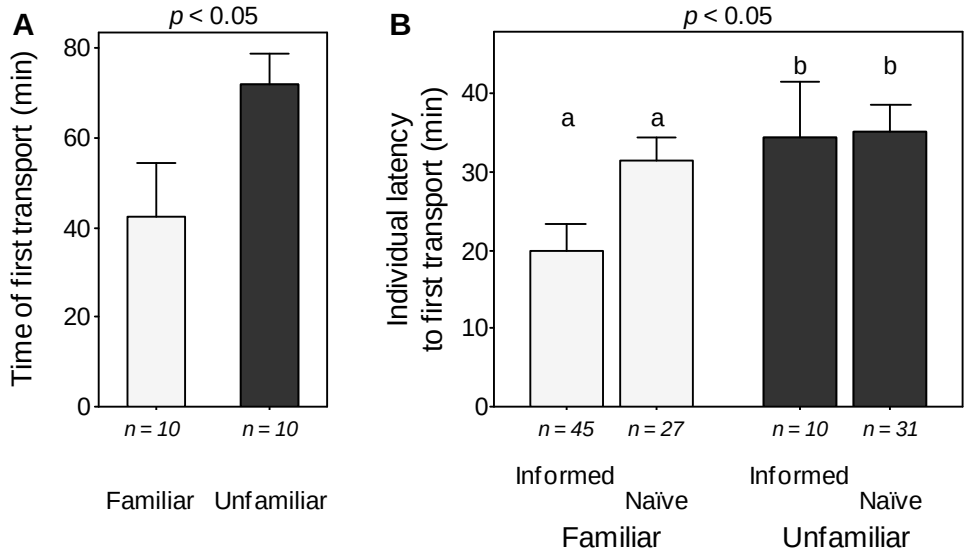

Figure IV.5 Transport
(A) Time of first transport to familiar (light grey) and unfamiliar (dark grey) nest sites (paired t-test; t = -2.307, df = 9, $p < 0.05$; normality of data: K.S. tests, familiar: KS = 0.193, df = 10, $p > 0.2$; unfamiliar: KS = 0.192, df = 10, $p > 0.2$). **(B)** Individual latencies to first transport to familiar and unfamiliar sites for informed and naïve carriers. Bars and whiskers represent means and standard errors, respectively. *P*-value is given for the effect of nest site on latencies (GLMM; log-transformation of latencies). Same letters indicate no differences, whereas different letters indicate significant differences ($p < 0.05$) in LSD post-hoc tests.

DISCUSSION

Our results show that informed individuals play a key role in the early steps of emigration to high-quality, familiar nest sites. Individuals which had visited the familiar site prior to emigration indeed possessed private information about its location. They were therefore more likely to head towards that site and were able to find it significantly faster than unfamiliar, novel nest sites. At this early stage, information seemed to remain private, as naïve workers which had not previously visited the familiar nest seemed unable to use that information and instead randomly explored the arena in search for suitable nest sites. Private information on the location of nest sites could correspond to either navigational memory, or individual-specific pheromone trails leading from the old nest to the familiar nest (see Aron *et al.* 1988 and Chapter V, Section A, p69 for more details). A correlation among informed workers between (i) the capability of efficiently locating the familiar nest, and (ii) the recency of the last visit to that site and/or the intensity of site exploration prior to emigration would be strong evidence for an involvement of individual memory (Aron *et al.* 1993; Grüter *et al.* 2010). No such correlation was observed; further investigations will therefore be necessary to disentangle the respective roles of memory-based navigation and chemical orientation (see Chapter V, Section A, p69).

The use of private information by informed workers resulted in (i) overrepresentation of informed workers among scouts at the familiar nest site, and (ii) earlier independent discoveries of the familiar nest site. This had a strong impact on the collective decision-making process by bringing forward the subsequent steps of emigration for the familiar nest. Indeed, both recruitment by tandem running and transport happened earlier for the familiar nest site. This resulted in familiar nests being preferred over unfamiliar nests in the' final choice of colonies, although this trend was not significant, possibly due to the low number of colonies used in this experiment (n = 10; exact binomial test: $p = 0.062$).

Tandem running did not appear to be influenced by prior information about the familiar site. Workers indeed led similar numbers of tandem runs to the familiar and to the unfamiliar site. Additionally, the earlier occurrence of tandem running to the familiar site was not due to differences in the behaviour of individual workers after entering either nest (i.e. likelihood of leading tandem runs and/or latency to first tandem running), but appeared to be a direct consequence of earlier discoveries of the familiar site by informed workers. By contrast, latency from discovery to first transport was lower for both informed and naïve individuals at the familiar than at the unfamiliar nest site. This observation, combined with the earlier discovery of the familiar site, may account for the earlier occurrence of transport at the familiar than at unfamiliar nest site. Additionally, this observation shows that (i) prior information about the familiar site influenced the timing of individual decisions to start

carrying, and (ii) that information was not exclusively private at that stage, but had been at least partially transferred from informed to naïve individuals.

Naïve workers could possibly use two non-exclusive types of social cues when assessing the familiar site, i.e. chemical cues and/or social interactions with nestmates. The nature of the cues involved will be investigated in detail in the next Chapter (see p83). The present experiment however already provides indirect support for the influence of social interactions on the commitment of naïve workers to the familiar nest. Several empirical and theoretical studies have indeed shown for *Temnothorax* sp. that full commitment to a nest is normally triggered when the nest population reaches a certain value, or quorum threshold (Dornhaus & Franks 2006; Franks *et al.* 2006a; Franks *et al.* 2003a; Marshall *et al.* 2009; Marshall *et al.* 2006; Pratt 2005; Pratt *et al.* 2002; Pratt & Sumpter 2006; Pratt *et al.* 2005; Sumpter & Pratt 2009). The use of private information by informed workers in the first stages of emigration is likely to result in the quorum threshold being reached earlier in the familiar site for two reasons: (i) there were usually a few workers (range 0-7, median 3) already present inside the familiar site at the onset of emigration, and (ii) the initial increase in the population should be faster for the familiar than for the unfamiliar nest site, because both independent discoveries and tandem running occur earlier. As a consequence, both naïve and informed workers can be expected to commit to the familiar site and start carrying there sooner than to the unfamiliar site, which will be slower in reaching a quorum threshold.

Although social cues were very likely to influence individual decisions while evaluating the nest, there was no clear evidence that informed workers also relied on private information during assessment. Indeed, although individual latency to first transport tended to be lower for informed than for naïve workers at the familiar site, this trend was not significant. This could indicate that private information does not play any role in individual assessment of familiar nest sites. However, the use of private information by informed workers may also have been merely masked by the concurrent use of social information by all workers. To discriminate between these two hypotheses, an experiment aimed at dissociating the effects of private and social information in nest assessment was performed and will be presented in the next chapter (see p83).

To summarise, the use of private information by informed workers resulted in familiar, high-quality available nest sites being discovered faster than novel, unfamiliar sites. This induced an earlier and a steeper initial increase in the population in familiar than unfamiliar nest sites. Transport therefore started earlier for familiar sites. This in turn influenced colonies' overall preference at the outcome of emigration. Informed workers therefore played a key role in organising the entire emigration process and directing colonies towards familiar, high-quality nest sites.

Specialised and well-informed individuals were already known occasionally to play a key role in organising division of labour in social insect colonies (Anderson & Ratnieks 1999; Fewell 2003; Gordon 2002; Jackson *et al.* 2006; O'Donnell & Bulova 2007; Robson & Traniello 1999). The present experiment demonstrates that this concept also applies to collective decision-making by social insects. Individuals are indeed not always equivalent, and asymmetric access to information can result in well-informed individuals being more influential and playing a key role in determining a colony's final decision. Results from Chapter II (see p11) indicate that in the case of emigrations by *T. albipennis*, this is beneficial for the colony as it can improve collective performance in terms of both speed and accuracy and contribute to group cohesion.

The key role played by informed individuals in orienting emigrating ant colonies can be compared to the key role played by informed leaders in influencing movement direction in groups of vertebrates travelling together (Couzin *et al.* 2005; Sumpter *et al.* 2008a; Sumpter 2006). In large vertebrate groups such as flocks of birds or fish schools, information can be efficiently transferred throughout the group via self-organised processes, whereby informed leaders use both private and social information, whereas naïve individuals rely mostly on social information to determine their position, speed and direction of movement (Couzin *et al.* 2005). In emigration by *T. albipennis*, it appears that information remains private during the first steps of emigration and is later transferred to naïve individuals. It is, however, still unclear whether sharing of information between workers relies only on self-organised social interactions, as it is the case for large vertebrate groups (Couzin *et al.* 2005; Sumpter *et al.* 2008a; Sumpter 2006), or whether it also involves active signalling by informed workers, as in smaller vertebrate groups (Boinski & Campbell 1995).

This chapter presented empirical evidence that both private and social information are used during emigrations to high-quality, familiar nest sites. In the next chapter, we will investigate in more detail the type of information stored by informed workers when visiting a high- or low-quality available nest site, and the mechanisms underlying the retrieval and sharing of information between informed and naïve individuals during emigrations.

Chapter V. Storage, Retrieval and Sharing of Information about Familiar Nest Sites in Ants

A- Navigation to high quality, familiar nest sites

ABSTRACT

Social insects can orient, in familiar areas, by using individual navigational memories or chemical orientation trails; the relative importance of these two strategies varies greatly both among and within species. In *Temnothorax* ants, workers have been shown to rely both on their memory and on individual-specific trails to travel between the nest and previously visited food sources. Here, we investigate whether *T. albipennis* ants rely more on memory or on chemical trails to navigate towards familiar, high-quality nest sites when there is a conflict between these two sources of information. Emigrating colonies that had previously familiarised themselves with one high-quality available nest site were faster at discovering that site than an equidistant, unfamiliar nest site. This was the case whether chemical cues had been rotated 180º (test) or not (control). Although the rotation of chemical cues occasionally induced transient confusion at the beginning of emigrations, navigation towards familiar nest sites appeared to be as efficient in test as in control colonies after that initial period of hesitation. These results indicate that visual-based navigational memory strongly dominates over the use of chemical cues in *T. albipennis* orientation towards familiar nest sites, in agreement with previous studies on the mechanisms of navigation towards food sources in related *Temnothorax* species.

INTRODUCTION

In previous chapters, it was shown that emigrating colonies of *Temnothorax albipennis* can retrieve and use information gathered by workers upon visits to available nest sites prior to emigration. In particular, during emigrations, informed workers were shown to travel effectively to previously visited, high-quality nest sites and found these familiar sites faster than by random exploration (see p60).

Orientation by individuals in familiar areas is well-documented in social insects, especially in the context of travelling between the nest and food sources in central place foragers. Workers are able to locate familiar, rewarding target sites by using two non-exclusive, complementary orientation mechanisms: chemical orientation and navigational memory (Anderson & McShea 2001; Beckers *et al.* 1989; Carroll & Janzen 1973; Collett & Collett 2002; Collett *et al.* 2003; Hölldobler 1978; Hölldobler & Wilson 1990; Jarau & Hrncir 2009; Wilson 1971).

Chemical orientation is used by a variety of social insect species (e.g. ants, termites, stingless bees) to direct a colony's workforce to profitable food sources (Hölldobler & Wilson 1990; Jarau 2009; Wilson 1971). Chemical trails laid between the nest and the target site help individuals orient and travel between the two locations. In most species relying on mass recruitment (e.g. among others army ants: Chadab & Rettenmeyer 1975; fire ants: Wilson 1962; Pharaoh's ants: Sudd 1960; Argentine ants: Aron *et al.* 1993), chemical trails are laid by experienced workers after a successful visit to a rewarding site and can subsequently be followed by both experienced and naïve individuals (Beckers *et al.* 1989). Such chemicals involved in communication between conspecifics qualify as pheromones (Hölldobler & Wilson 1990). Mass recruitment through pheromone trails is particularly advantageous when several food sources of different qualities are discovered, or when several alternative paths to a given source exist. Positive feedback and down-regulating mechanisms in trail laying and following behaviours allow colonies to select collectively the most profitable food source and/or the most efficient path to the source (Beckers *et al.* 1992a; Beckers *et al.* 1992b; Beckers *et al.* 1993; Beckers *et al.* 1990; Bonabeau *et al.* 1997; Camazine *et al.* 2001; Detrain & Deneubourg 2008; Goss *et al.* 1989; Robinson *et al.* 2008; Stickland *et al.* 1999; Vittori *et al.* 2006).

Social insects also rely on individual memories to navigate in well-known areas (Collett & Collett 2002; Collett & Graham 2004; Collett *et al.* 2003; Collett *et al.* 2006). For example, ants commonly use memories of visual landmarks (Durier *et al.* 2003; Fukushi & Wehner 2004; Harris *et al.* 2007; Judd & Collett 1998), odour landmarks (Steck *et al.* 2009; Steck *et al.* 2010) or geometrical features (Wystrach & Beugnon 2009), path integration (Andel & Wehner 2004; Collett & Collett 2000a; Collett & Collett 2000b), sun compass orientation (Muller & Wehner 2007; Wehner & Muller 2006) and motor memories (Knaden *et al.* 2006; Lent *et al.* 2009; Sommer & Wehner 2005) to locate and travel between the nest and familiar foraging sites.

Most social insects combine the use of both individual navigational memories (private information) and chemical orientation (usually social information) to orient efficiently in familiar environments. However, the relative degree to which they rely on memory vs. chemicals varies greatly between species (see e.g. Aron *et al.* 1993; Aron *et al.* 1988; Cosens & Toussaint 1985; Evison *et al.* 2008; Fourcassie & Beugnon 1988; Grüter *et al.* 2010; Harrison *et al.* 1989; Henquell & Abdi 1981; Hölldobler 1976; Hölldobler *et al.* 1974; Klotz & Reid 1992; Möglich & Hölldobler 1975; Rosengren & Fortelius 1986; Salo & Rosengren 2001; Traniello 1989; Vilela *et al.* 1987); it can range from the almost exclusive use of individual navigation (e.g. in honeybees and desert ants) to the almost exclusive use of pheromone trails (e.g. trunk trail recruiting ants). In particular, the relative use of memory

vs. chemical orientation cues in ants depends on many factors, such as experience, colony size, spatial and temporal heterogeneity of food sources, ecological conditions, and many other factors (Aron *et al.* 1993; Grüter *et al.* 2010). For example, mass pheromone trail recruitment is favoured in large colonies whereas individual navigation predominates in smaller colonies, both within (Mailleux *et al.* 2003; O'Donnell & Bulova 2007) and between species (Anderson & McShea 2001; Beckers *et al.* 1989). Another important factor is the stability of resources. Highly predictable food sources, e.g. favour the use of memory, leading to individual specialisation on specific sites and spatial fidelity (Aron *et al.* 1993; Beverly *et al.* 2009; Grüter *et al.* 2010; Quinet & Pasteels 1996; Rosengren 1971; Rosengren & Fortelius 1986; Traniello 1977). Habitat characteristics can also influence the preferred orientation strategy: e.g. desert ants cannot use pheromone trails, because ant-laid chemicals are not stable enough on high-temperature grounds (Ruano *et al.* 2000); whereas the use of memory can be hindered by the spatial complexity of certain multi-bifurcation routes (Grüter *et al.* 2010).

Similarly, the recruitment methods and mechanisms underlying the transfer of information from experienced to naïve individuals are highly variable (Beckers *et al.* 1989; Hölldobler & Wilson 1990). In some species of ants, naïve workers can be directed to new food sources by following pheromone trails laid by experienced workers (Aron *et al.* 1993; Beckers *et al.* 1992a; Chadab & Rettenmeyer 1975; Dussutour *et al.* 2009; Hölldobler 1976; Jessen & Maschwitz 1986; Sudd 1960; Traniello 1977; Wilson 1962). By contrast, in other species naïve individuals do not follow trails laid by their nestmates (Aron *et al.* 1988). In such cases recruitment occurs mainly by tandem running, a slow, one-to-one recruitment method whereby an experienced individual leads a naïve follower to a site of interest, so that the follower can learn the route between the nest and the target site (Franks & Richardson 2006; Richardson *et al.* 2007). Recruitment by tandem running is frequent in species with small colonies, such as ants of the genus *Temnothorax* (Möglich 1978; Möglich 1979; Möglich *et al.* 1974).

Temnothorax ants mostly use individual foraging and exploration strategies, and have been shown to use visual landmarks when navigating in familiar environments (Aron *et al.* 1988; McLeman *et al.* 2002; Pratt *et al.* 2001). However, workers also lay chemical trails that help them orient between the nest and a food source (Aron *et al.* 1988; Lane 1977), or between the old nest and the new nest during an emigration (Maschwitz *et al.* 1986). Chemical trails in *Temnothorax* differ from those used in many other ant species, because they are individual-specific: they are followed almost exclusively by the specific workers that laid them (Aron *et al.* 1988; Maschwitz *et al.* 1986). Such individual-specific trails can occasionally be followed by other experienced workers, but have not been observed to

initiate recruitment of new, naïve individuals (Aron *et al.* 1988). Additionally, individual-specific chemicals have been shown to play a role in size assessment of potential new nest sites by exploring workers during emigrations (Mallon & Franks 2000; Mugford *et al.* 2001). In *Temnothorax* species, the use of chemical trails to navigate and to evaluate a new nest site does therefore not necessarily involve social information, but could also correspond to some form of private information, depending on the specificity of the chemicals involved.

Chapter IV highlighted the importance of experienced *T. albipennis* workers relying on private information to find rapidly high-quality, familiar nest sites during emigrations. Such private information could be stored either internally, in the memories of informed workers, or externally, in the form of individual-specific chemical trails. To discriminate between these two hypotheses, a conflict between visual and potential chemical cues was imposed experimentally during an emigration to a familiar and an unfamiliar identical, high-quality nest sites. Such informational conflicts have been used in previous studies on other ant species to determine the type of information predominantly used by individuals (Aron *et al.* 1993; Grüter *et al.* 2010; Harrison *et al.* 1989; Hölldobler 1976; Rosengren & Fortelius 1986; Salo & Rosengren 2001). This approach was preferred to simply removing all chemical cues, because *Temnothorax* ants are known to mark chemically familiar areas, and behave differently when placed on a fresh, unfamiliar substrate (Aron *et al.* 1986). Preliminary experiments where all chemicals were removed just before inducing emigrations indicated that the ants were strongly disturbed by the manipulation and hesitated to walk on fresh surfaces when their old nest had been damaged. This was also observed in previous studies on *T. albipennis* where acetate sheets covering the floors were removed at the onset of emigrations (McLeman *et al.* 2002; Pratt *et al.* 2001). A simple 180° rotation of the substrate was therefore considered preferable to investigate the ants' behaviour in less disturbing conditions.

Two different experiments were run. It is known that *Temnothorax* species use both visual landmarks and menotactic orientation (i.e. setting the travelling direction at a certain angle with a directional light stimulus) when travelling between the nest and food sources or new nest sites (Aron *et al.* 1988; McLeman *et al.* 2002; Pratt *et al.* 2001). In the present experimental conditions, however, it was not known whether the ants relied more on local landmarks (i.e. landmarks provided inside the exploration arena) or on more distant landmarks, such as prominent features in the laboratory or the direction of sun light. In the first experiment, local landmarks of different shapes were interspersed between the old nest and the familiar and unfamiliar nests. Just before emigration, all potential trails were rotated 180°, but the landmarks were left at the same position to provide a constant visual landscape. However, workers may also have chemically marked the local landmarks

themselves during exploration. In that case landmarks would not only provide visual information, but could also act as chemical orientation cues. To control for this eventuality, a second experiment was run where pairs of identical landmarks were placed symmetrically within the arena between the old nest and the familiar nest on one hand, and between the old nest and the unfamiliar nest on the other hand. Just before emigration, all potential trails were rotated 180°, and landmarks were also rotated and swapped between both branches of the arena. Because of the symmetrical arrangements of the landmarks; the visual landscape provided in the second experiment was also constant; but the entire chemical landscape was rotated.

Rotation of the chemical landscape while maintaining a constant visual landscape had little effect on workers' abilities to quickly locate the familiar nest. This suggested that visual navigational memory strongly dominates over chemical orientation for experienced individuals travelling between the old nest and the familiar nest.

METHODS

Experimental design

Two similar experiments ('Trail rotation' and 'Chemical landscape rotation') were performed to investigate the potential role of chemical trails and landmark chemical marking in ant navigation to familiar nest sites.

Experiments were carried out in the geometrically complex arenas described in Chapter II (Figure II.1, see p15). In both experiments, the floors of all dishes and tunnels were covered with fitted acetate sheets (Figure V.1). In experiment 'Trail rotation', landmarks of different shapes were interspersed in the two branches of the arena, as shown in Figure II.1 (p15). By contrast, in experiment 'Chemical landscape rotation', pairs of identical landmarks were placed symmetrically in both branches of the arena, so that workers would encounter the same succession of shapes when going from the centre to either peripheral dish (Figure V.1). Colonies housed in good nests (see p14) were positioned in the middle of the central dish and were allowed to explore the set-up for one week; throughout exploration, colonies could familiarise themselves with one available, good nest site identical to their home nest, positioned at one end of the arena.

At the end of exploration, all acetate sheets and landmarks were lifted from the arena. In control conditions, they were then replaced exactly as before, serving as a control for experimental disturbance. In test conditions, acetate sheets were rotated 180° and swapped between opposite branches of the arena, so that any trails previously leading from the old

nest to the familiar nest would now lead from the old nest to the opposite end of the arena (Figure V.1). In the experiment ‘Trail rotation’, landmarks were replaced exactly as during exploration, so that only floor marking chemicals (and thus potential trails) were rotated. By contrast, in the experiment ‘Chemical landscape rotation’, symmetrical landmarks were also rotated 180° and swapped between both branches of the arena, so that the entire chemical landscape was rotated. Colonies were then immediately induced to emigrate and had to *choose between the familiar site and an identical, unfamiliar nest site* introduced at the other end of the arena at the onset of emigration (Figure V.1).

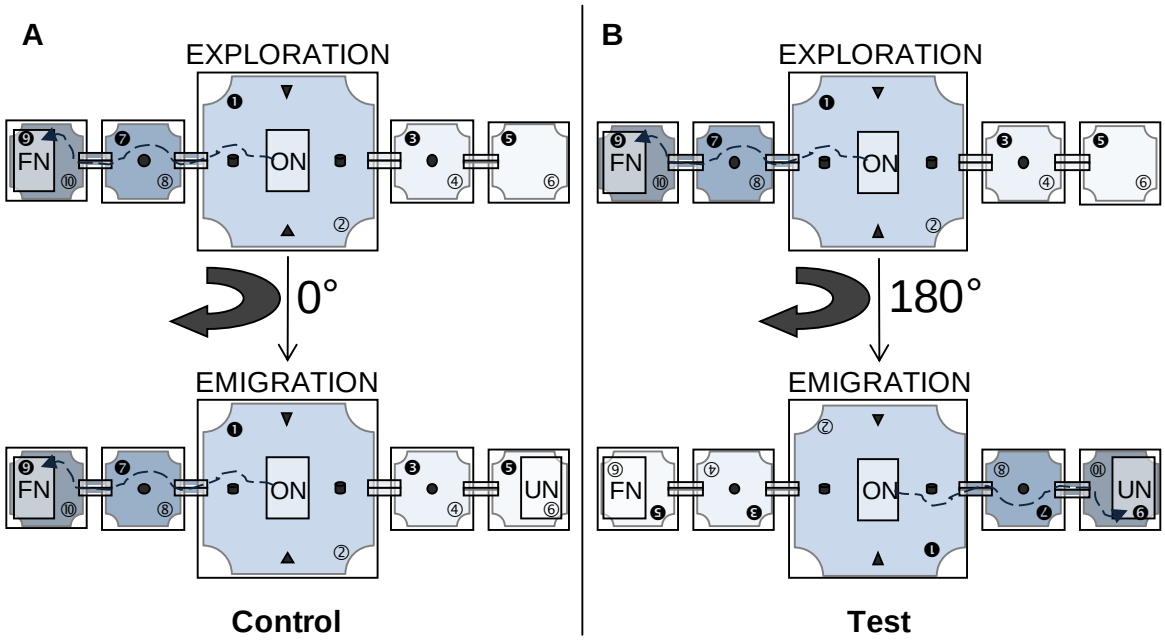

Figure V.1 Experimental design

Experimental design used for experiments ‘Trail rotation’ and ‘Chemical landscape rotation’. Shaded polygons represent the acetate sheets covering the floor of the exploration arena (described in Figure II.1, see p15). Landmarks are shown in the symmetrical arrangement used for experiment ‘Chemical landscape rotation’. Individual acetate sheets each have a unique colour and combination of numeric marks, making their position and orientation easy to detect. The broken arrow represents a hypothetical chemical trail laid between the old nest (ON) and the familiar nest (FN) during exploration. UN represents the position of the unfamiliar nest during emigration. In the control, acetate sheets and landmarks were lifted and replaced at exactly the same position at the onset of emigration (0º rotation). In the test, acetate sheets were rotated 180º and swapped between opposite branches of the arena at the onset of emigration, so that any chemical trails were entirely rotated 180º. Depending on the experiment, landmarks were or were not also rotated and swapped between opposite branches of arena.

Data recording and analysis

Emigrations were observed until both new nest sites were discovered. The times at which intermediate, peripheral dishes and new nests were first entered by a worker were recorded. This allowed the determination, for each nest, of the following variables: (1) *discovery time* (see Chapter II, p17), and (2) its three exploration-related components: (i) *time to leave the central dish* (i.e. time interval between the destruction of the old nest and the first entrance in the intermediate dish, 'ON to I'); (ii) *crossing time of the intermediate dish* (i.e. time interval between the first entrance in the intermediate dish and the first entrance in the peripheral dish, 'I to P'); and (iii) *nest entrance localisation time* (i.e. time interval between the first entrance in the peripheral dish and the first entrance in the new nest, 'P to NN'). Additionally, *emigration time*, and *the proportion of colony items observed in the familiar nest* were recorded at the end of emigration for each colony, as explained in Chapter II (see p17).

Colonies that displayed little activity during the exploration period and colonies that emigrated to the new nest site were excluded from the final analyses as explained in Chapter II (see p16). The total numbers of colonies included in final analyses were 15 in experiment 'Trail rotation' and 17 in experiment 'Chemical landscape rotation'. In both experiments, each colony was tested once under control and once under test conditions; half of the colonies received the 'control' treatment first, whereas the other half received the 'test' treatment first.

Statistical analyses

Emigration time and colony distribution at the end of emigration (i.e. proportion of the colony in the familiar nest) were compared among treatments using SPSS general linear mixed model procedure (GLMM) with fixed factor 'Treatment' (0º vs. 180º) and random factors 'Colony' and 'Block'. Discovery time and exploration variables (i.e. 'ON to I' 'I to P' and 'P to NN') were compared among nests and treatments using a GLMM procedure with fixed factors 'Treatment', 'New nest site' (familiar vs. unfamiliar) and their interaction, and random factors 'Colony' and 'Block'. We selected the model fitting our data best by using a stepwise backward procedure. Statistical significance was tested using an Analysis of Deviance with a Type III Sum of Squares method (comparison of the full model to the full model without the factor of interest). Normality and homoscedasticity of residuals were checked using Kolmogorov-Smirnov and Levene's tests. If residuals were not normally distributed, we applied either log- or power-transformation to the data.

RESULTS

Experiment 'Trail rotation'

Colonies emigrating to a familiar and an unfamiliar nest showed no differences in overall emigration time whether potential chemical trails had been rotated 180º (test) or not (control; Figure V.2 A; GLMM, effect of treatment: $F_{1,9} = 0.337$, $p = 0.58$). Colony distribution at the end of emigration was similar for both treatments and colonies overall preferred the familiar over the unfamiliar nest (Figure V.2 A; GLMM, effect of treatment: $F_{1,9} = 1.702$, $p = 0.22$; 1-sample Wilcoxon test on pooled data, n = 30, $p < 0.001$). Swapping potential chemical trails therefore did not have an effect on colony performance.

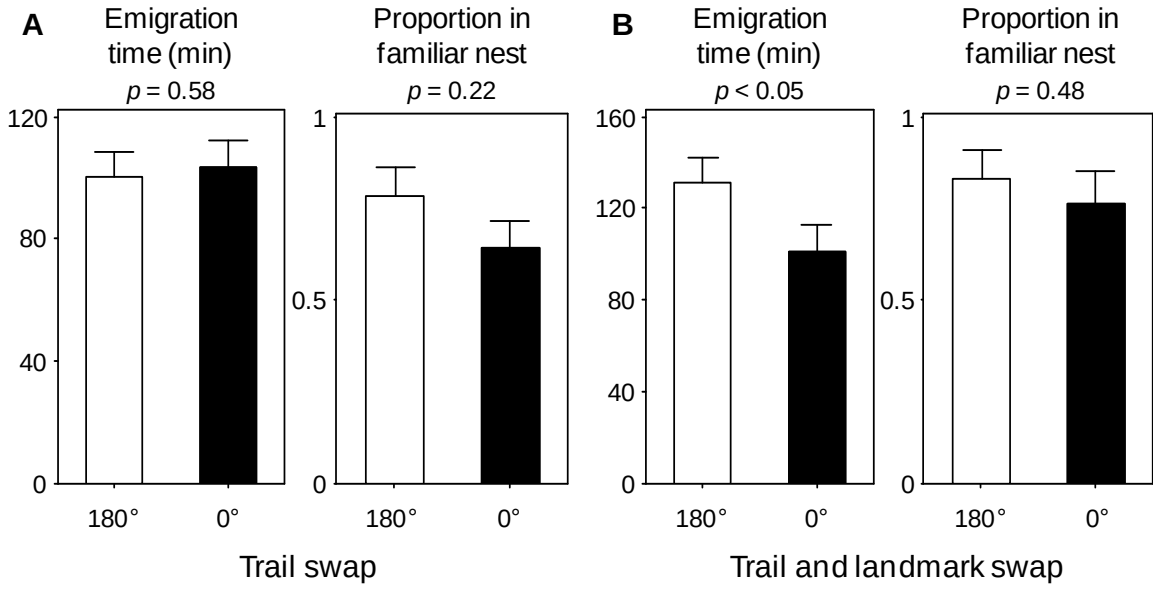

Figure V.2 Collective emigration performance

Emigration time and proportion of the colony in the familiar site for test (white bars; 180º rotation) and control (black bars; 0º rotation) colonies in experiments 'Trail rotation' (n = 15; **(A)**) and 'Chemical landscape rotation' (n = 17; **(B)**). Bars and whiskers represent means and standard errors, respectively. *P*-values are given for the effect of treatment on all variables (GLMM; no data transformation).

Additionally, test and control colonies did not differ in the discovery times of either nest or in their exploration dynamics (Figure V.3 A; GLMM, interaction nest x treatment: $F_{2,36} \leq 1.53$, $p > 0.2$ for all variables; effect of treatment: $F_{1,37} \leq 2.553$, $p > 0.1$ for all variables). In both treatments, familiar sites were discovered significantly earlier than unfamiliar sites (Figure V.3 A; GLMM, effect of nest: $F_{1,36} = 28.456$, $p < 0.001$). This was due to workers crossing intermediate dishes leading to the familiar nest faster than those leading to the unfamiliar nest (Figure V.3 A; 'I to P', GLMM, effect of nest: $F_{1,37} = 20.128$, $p < 0.001$), and locating the nest entrance faster for familiar than for unfamiliar nest sites (Figure V.3 A; 'P to NN' GLMM, effect of nest: $F_{1,37} = 18.279$, $p < 0.001$). By contrast, the time taken to leave the central arena was similar in both directions (Figure V.3 A; 'ON to I' GLMM, effect of nest: $F_{1,37}$

= 1.320, p = 0.25) and can be considered as a 'reaction time', i.e. the time necessary for scouts to start searching for suitable nest sites after destruction of their old nest.

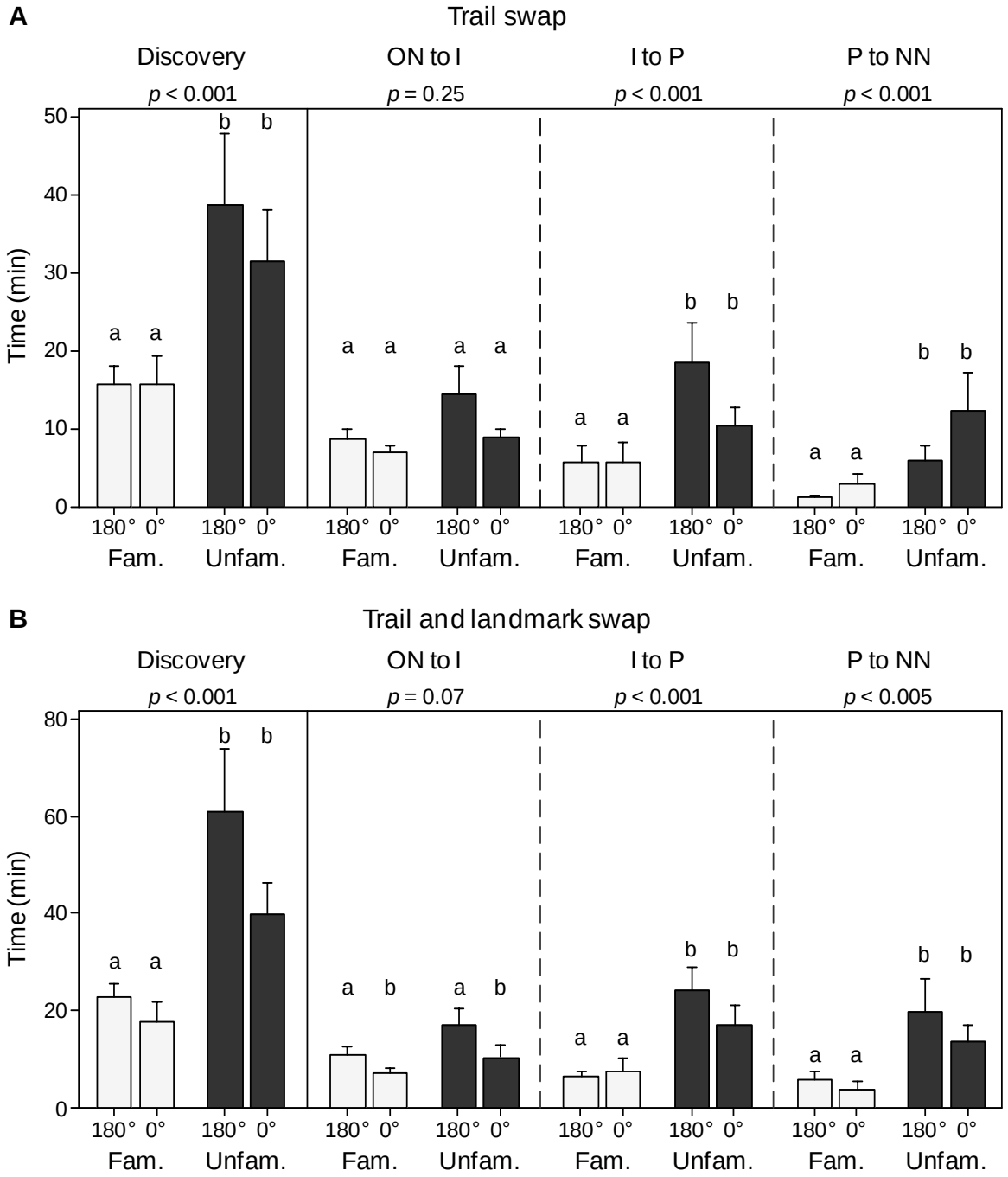

Figure V.3 Exploration dynamics and discovery times

Discovery time, time to leave the central dish (ON to I), crossing time of the intermediate dish (I to P), and nest entrance localisation time (P to NN) of the familiar (Fam., light grey bars) and unfamiliar (Unfam., dark grey bars) new nest sites for test (180º rotation) and control (0º rotation) colonies in experiments 'Trail rotation' (n = 15; **(A)**) and 'Chemical landscape rotation' (n = 17; **(B)**). Bars and whiskers represent means and standard errors, respectively. *P*-values are given for the effect of nest site on all variables (GLMM; Log-transformation of all variables). Same letters indicate no statistical differences, whereas different letters indicate significant differences between categories.

Overall, rotating potential chemical trails 180º therefore did not affect the colonies' ability efficiently to find familiar, suitable nest sites. However, this does not entirely rule out the involvement of chemical cues in navigation from the old nest to the familiar nest, as landmarks were left in their original position and may themselves be marked with chemical cues.

Experiment 'Chemical landscape rotation'

Colonies emigrating to a familiar and an unfamiliar nest were significantly faster when potential chemical trails and landmarks had not been rotated (control) than when they were both rotated 180º (test; Figure V.2 B; GLMM, effect of treatment: $F_{1,14} = 5.801$, $p < 0.05$). Colony distribution at the end of emigration was however similar for both treatments (Figure V.2 B; GLMM, effect of treatment: $F_{1,14} = 0.539$, $p = 0.48$) and colonies overall preferred the familiar over the unfamiliar nest (Figure V.2 B; 1-sample Wilcoxon test on pooled data, n = 34, $p < 0.001$). Swapping potential chemical trails and landmarks therefore affected emigration dynamics, but not the colony's final nest choice.

The longer emigration time observed for test colonies was likely to be partly due to differences in 'reaction time' between treatments. Test colonies were indeed significantly slower to leave the central arena in test than in control conditions (Figure V.3 B; 'ON to I' GLMM, effect of treatment: $F_{1,46} = 5.141$, $p < 0.05$), although they were as slow to leave the central arena in both directions (Figure V.3 B; 'ON to I' GLMM, interaction nest x treatment: $F_{1,45} = 0.263$, $p = 0.61$; effect of nest: $F_{1,46} = 3.482$, $p = 0.07$). This indicates that test colonies were initially disturbed by the experimental rotation of trails and landmarks at the beginning of emigration, which increased their overall reaction time.

By contrast, test and control colonies did not differ in the crossing times of intermediate dishes or in the time to locate the nest entrance for either nest (Figure V.3 B; GLMM, interaction nest x treatment: $F_{1,44} \leq 1.727$, $p > 0.19$ for both variables; effect of treatment: $F_{1,44} \leq 1.451$, $p > 0.23$ for both variables). In both treatments, intermediate dishes leading to the familiar nest were crossed faster than those leading to the unfamiliar nest (Figure V.3 B; 'I to P', GLMM, effect of nest: $F_{1,45} = 14.071$, $p < 0.001$), and nest entrance was located faster for familiar than for unfamiliar nest sites (Figure V.3 B; 'P to NN' GLMM, effect of nest: $F_{1,44} = 16.546$, $p < 0.001$).

The higher reaction times observed in test colonies resulted in both familiar and unfamiliar nests being discovered slightly later in test than in control colonies, although this trend was not significant (Figure V.3 B; GLMM, effect of treatment: $F_{1,47} = 3.704$, $p = 0.06$). However, in both treatments familiar nests were discovered significantly earlier than

unfamiliar nests (Figure V.3 B; GLMM, interaction $F_{1,46} = 1.284$, treatment x nest: $p = 0.26$; effect of nest: $F_{1,47} = 18.726$, $p < 0.001$)

These results indicate that colonies are sensitive to chemical cues in their environment, since rotating the acetate sheets and landmarks 180º resulted in workers hesitating longer before starting to search for new nest sites. However, the rotation of chemical cues did not affect colonies' ability to locate efficiently familiar, suitable nest sites after this initial hesitation period. Overall, the results of this and the previous experiments therefore show that chemical trails and chemical marking of landmarks do not play a major role in navigation between the old nest and the familiar nest. This strongly suggests that workers rely on visual cues instead.

DISCUSSION

When the visual landscape was constant, 180° rotation of the chemically marked floors (experiment 'Trail rotation') or of the entire chemical landscape (experiment 'Chemical landscape rotation') (i) did not impair the ability of workers to discover the familiar nest earlier than the unfamiliar nest during emigrations, and (ii) did not modify colonies' overall preference for the familiar nest. Closer examination of the exploration pattern revealed that after scouts had left the central dish containing the old nest, they headed towards the familiar nest (intermediate dish crossing time) and were able to locate its entrance faster than for the unfamiliar nest, whether chemical cues had been rotated (test) or replaced exactly as before (control). These results indicate that neither chemical trails nor chemical marking of landmarks played a major role in worker navigation between the old nest and the familiar nest. Navigational memory based on visual cues therefore clearly dominated over chemical orientation. These results are in agreement with previous studies on *T. albipennis* and other closely related *Temnothorax* species, showing that workers use visual cues to travel between the home nest and food sources (Aron *et al.* 1988) or between the old nest and new nest sites during emigrations (McLeman *et al.* 2002; Pratt *et al.* 2001), and that visual navigation clearly overrides chemical orientation when these two sources of information are conflicting (Aron *et al.* 1988). Similar results were obtained in mass recruiting ant species with intermediate colony size, such as *Lasius niger* (Aron *et al.* 1993; Grüter *et al.* 2010).

In one of the two experiments, ('Chemical landscape rotation'), 180° rotation of the chemical landscape induced an initial confusion period (longer 'reaction time') which resulted in overall slower emigration, whereas in the other experiment ('Trail rotation'), such confusion was not observed. The difference between the two experiments could be due to a specific role played by the chemical marking of landmarks, but this is unlikely. Indeed, if chemical

marking of landmarks was of such importance, then the swap of landmarks would be expected to also affect the crossing times of intermediate dishes, which contained one landmark each (Figure V.1). However, this was not observed: crossing times were similar in test and control conditions. The initial confusion observed in experiment 'Chemical landscape rotation' is therefore more likely to be due to the rotation of chemical cues in the central arena. Indeed, *Temnothorax* sp. chemically mark familiar areas, and alter their behaviour when these marks are removed (Aron *et al.* 1986). Here, the displacement of familiar chemical cues may have induced scouts in test colonies to hesitate before starting their search for new nest sites. Why, then, was such initial confusion not observed in the experiment 'Trail rotation'? The two experiments were performed at different times of the year (winter vs. spring), with two distinct sets of colonies differing in collecting dates, experience in the lab and colony sizes. These factors are known to affect marking behaviour of familiar areas (Aron *et al.* 1986), and could explain why the experimental manipulation had more impact on test colonies in one of the two experiments.

Additionally, the longer 'reaction time' observed in test colonies in the experiment 'Chemical landscape rotation' is unlikely to be due to a conflict between visual and chemical cues regarding the location of the familiar nest. Indeed, test colonies were only slower than control colonies in the initial stage of emigration, within the central dish containing the old nest; at that early stage, there was no evidence that workers used information about the location of the familiar nest: tunnels leading to either direction were indeed always crossed at similar times, whether chemical cues had been rotated or not. Once workers had left the central dish, by contrast, test colonies were as fast to cross the intermediate dish leading to the familiar site and locate the familiar nest entrance as control colonies in both experiments. This indicates that at the time when workers made use of their information on the location of the familiar nest (i.e. after leaving the central dish), rotating chemical cues (and thus imposing an informational conflict between visual and chemical cues) did not affect travelling speed to the familiar site. This suggests that chemical orientation plays little role in helping ants navigate towards the familiar site. These results agree with a recent study on *Lasius niger*, showing that experimentally induced informational conflict at trail bifurcations had no effect on the decision time of experienced workers heading in the 'correct' (i.e. previously rewarding) direction (Grüter *et al.* 2010).

By contrast, these results are in apparent contradiction with a previous study on a related *Temnothorax* species, indicating that colony and individual-specific chemical trails play an important role in orientation of transporters travelling between the old nest and the new nest during nest emigrations (Maschwitz *et al.* 1986). The difference between these two studies could be due to the fact that they consider different stages of emigration, namely

exploration in search for suitable new sites in the present study vs. transport in the previous study. It could be that vision by transporters is impaired because carried adults or brood items partially obstruct their visual field (Möglich 1978). Visual navigation would therefore be less effective, thus making necessary the use of chemical orientation during transport. Another possible explanation lies in the variation in workers' experience prior to emigration. In the study by Maschwitz *et al.* (1986), emigrations took place in an unfamiliar environment. By contrast, in the present study workers had familiarised themselves with the arena and the familiar nest for one week before emigration. In other species, it has been argued that chemical orientation plays an important role initially, during the first trips between the nest and a target site, serving as a guide while workers are learning the landmarks. The importance of chemicals then decreases over time as individuals rely more and more on navigational memory (Aron *et al.* 1993; Traniello 1989; Traniello & Levings 1986). According to this hypothesis, emigrations in unfamiliar arenas (as in the study by Maschwitz *et al.* 1986) would favour the use of chemical orientation whereas emigrations in familiar arenas and towards a familiar nest (as in the present study) would favour the use of navigational memory. Further experiments where the duration of the pre-emigration exploration period is varied may help test this hypothesis, and determine whether chemical orientation indeed plays a more important role early on in the familiarisation process.

The results presented above clearly indicate that navigational memory strongly dominates over the use of chemical cues in *T. albipennis* orientation between the old nest and a suitable, familiar nest. Why is this the case? Several hypotheses can be proposed to explain this observation. It could be that, as suggested by Grüter et al. (2010), chemical orientation is more time-consuming than visual navigation because it requires workers to keep their antennae close to the ground to detect chemicals. The use of memory would therefore allow experienced workers to travel faster to the familiar nest. Alternatively, memory could be more reliable than chemical cues when navigating towards a target site (Grüter *et al.* 2010). Indeed, because chemical trails are mostly individual-specific in *Temnothorax* and are not used to recruit new, naïve workers (Aron *et al.* 1988; Maschwitz *et al.* 1986), they are not reinforced by other individuals and remain at low concentration. Consequently, these trails may be lost easily, e.g. due to wind or rain or because they are laid on labile substrates. Chemical trails are therefore likely to be less durable than memories of prominent, stable landmarks and/or the use of sky compass or path integration. Additionally, it has been shown in many ant species that long exploration times combined with high stability and predictability of resources usually promote the use of memory and individual navigation strategies, resulting in individual specialisation on certain sites and high site fidelity (Aron *et al.* 1993; Beverly *et al.* 2009; Grüter *et al.* 2010; Quinet & Pasteels 1996; Rosengren 1971; Rosengren & Fortelius 1986; Traniello 1977). In the present context, the

resources are available nest sites, which are relatively stable and durable, thus explaining why individual memory may be favoured. Finally, the prominent role of memory could be due to ecological reasons. *Temnothorax* species usually have small colonies (typically much fewer than 500 workers) (Aron *et al.* 1986; Dornhaus & Franks 2006; Franks *et al.* 2006a; Möglich 1978; Partridge *et al.* 1997). This is thought to promote individual navigation strategies and one-to-one recruitment methods such as tandem running (Anderson & McShea 2001; Beckers *et al.* 1989; Mailleux *et al.* 2003; O'Donnell & Bulova 2007); indeed naïve workers usually do not follow trails laid by their nestmates in *Temnothorax* species (Aron *et al.* 1988). Laying chemical trails between the old nest and the familiar nest is therefore unlikely to help new, naïve individuals discover the site. Indeed, in Chapter IV, there was no evidence that naïve individuals benefited from the experience of informed workers when searching for new nest sites (see p60). Trail-laying by experienced worker would therefore not bring any additional recruitment advantage as it does in other species (see e.g. Grüter *et al.* 2010), and may therefore be restrained. This may also partly explain why chemical orientation appears to play such a small role in navigation to familiar nest sites in *T. albipennis*.

In conclusion, in the early stages of emigration, experienced *T. albipennis* workers appear to rely almost exclusively on visual memory when navigating towards previously visited, high-quality nest sites. It is not known, however, what specific form or forms of visual navigation are involved: memories of visual landmarks and/or geometrical features, menotactic orientation, path integration and use of sky compass are among the many mechanisms underlying ant visual navigation. Further experiments will help determine how *T. albipennis* navigate to familiar nest sites in more detail.

Individual memory appears to play a major role in the discovery of familiar, suitable nest sites; however, different mechanisms may underlie the subsequent assessment of these sites in experienced colonies. The next sections in this chapter aim at investigating these mechanisms in more detail, and evaluating the relative roles of social and private information in the evaluation of familiar nest sites.

B- Assessment of high quality, familiar nest sites

ABSTRACT

Temnothorax albipennis **have been shown to expedite decisions about high-quality, familiar nest sites at both the collective and the individual level, thus leading to improved collective performance during emigrations. Although both informed and naïve individuals appear to accept familiar good sites more readily than otherwise identical, novel sites, the detailed mechanisms underlying individual evaluation and information transfer among workers during nest assessment are still unclear. Here, we examine several hypotheses to account for these observations. We first show that although the nest population does increase faster in familiar than in unfamiliar nest sites, social interactions and quorum sensing alone cannot fully account for the quicker assessment of familiar sites. We then show that chemical marking of previously visited nest sites helps expedite decisions by both informed and naïve colonies. Pheromone communication therefore plays a role in the transfer of information from experienced to naïve workers during nest evaluation, together with other social interactions. Finally, we provide strong evidence that individual memory contributes to the earlier commitment of informed workers to high-quality, familiar nest sites. Overall, the quicker assessment of familiar sites derives from a complex interplay between these three sources of information. The implications of these findings are then discussed with regards to (i) the role of quorum sensing in group decision-making, (ii) the relative importance of independent evaluations vs. transfer of valuable information in nest site selection by ants, and (iii) the influence of individual memories on collective processes.**

INTRODUCTION

Living in groups can confer many benefits, such as reduced predation risk, lower energetic costs or increased foraging efficiency (Krause & Ruxton 2002). Another great advantage lies in collective decision-making abilities of animal groups, which may enable them to solve highly complex tasks (Couzin 2007; Krause *et al.* 2010). Shared decisions made through the collation of information among several group members are usually more accurate than decisions made by isolated individuals. This is known as 'collective wisdom' or 'the wisdom of crowds' (Conradt & Roper 2005; King & Cowlishaw 2007; List 2004; Simons 2004; Sumpter *et al.* 2008b; Sumpter & Pratt 2009; Surowiecki 2004) and is part of what has been named 'Swarm Intelligence' (Bonabeau *et al.* 1999a; Krause *et al.* 2010). A prerequisite for enhanced accuracy of collective choices is that every group member gathers information and makes a decision independently. If this assumption is invalid, collective processes may amplify informational biases or propagate initial errors, and thus lead to mistakes (Giraldeau *et al.* 2002; Sumpter & Pratt 2009; Surowiecki 2004). The condition of independence of individual choices to ensure high accuracy of collective decisions may seem paradoxical, as sharing of information among group members is necessary to reach a consensus (Conradt & Roper 2005; Sumpter & Pratt 2009). This may however be resolved if individuals each make a personal, independent assessment before opinion collation occurs. This strategy, proposed to limit the risk of biased decisions due to reciprocal influences among group members in

humans ('groupthink', see Janis 1972; Sumpter & Pratt 2009), is apparently implemented in natural collective decision-making processes such as nest site selection by house-hunting social insects (honeybees and ants of the genus *Temnothorax).* During swarming (honeybees) or emigrations (ants), individual scouts independently assess candidate sites before initiating recruitment of nestmates to these sites. Decisions are then made when the number of recruits inside a candidate nest site reaches a certain value, or quorum threshold (Franks *et al.* 2002; Pratt 2005; Pratt *et al.* 2002; Pratt *et al.* 2005; Seeley & Visscher 2003; Seeley & Visscher 2004a; Seeley & Visscher 2004b; Seeley *et al.* 2006; Sumpter & Pratt 2009; Visscher 2007; von Frisch 1923). This mechanism for opinion polling appears to be effective, as both naïve honeybee swarms and ant colonies are able to choose reliably and accurately between several nest sites in normal (i.e. non-emergency) conditions (Franks *et al.* 2006b; Franks *et al.* 2003b; Seeley & Buhrman 2001).

Although independent evaluations by scouts may ensure accurate collective decisions, emigrating ant colonies also greatly benefit from the use of information about available nest sites gathered by exploring workers prior to emigrations (see Chapter II and Chapter III, p11 and p31). In particular, information about high-quality nest sites was shown initially to remain private, then to be transferred to naïve workers during the assessment phase (see Chapter IV, p53), thus influencing decision-making by the entire colony. This is in apparent contradiction with the principle of independent individual assessment, but the advantages resulting from valuable information transfer may outweigh the risk of decision mistakes at the colony level (see Chapter III). Here my aim is to investigate how information is shared among individuals during assessment of familiar nest sites, and whether it violates the principle of independent evaluation.

As suggested in Chapter IV (see p66), a simple explanation could account for the lower assessment times observed for good familiar nest sites both at the colony-level (see Chapter II, p19) and at the individual-level (see Chapter IV, p64). Indeed, the initial presence of workers and early independent discoveries of the familiar nest site are expected to bring forward population increase in that site, so that the quorum threshold is reached earlier than for an unfamiliar site. Because quorum sensing controls the timing of the switch from nest assessment to full commitment and transport (Pratt 2005; Pratt *et al.* 2002), this process could suffice to explain the above observations without workers exploiting any information about site quality during evaluation. However, evidence for the role of social interactions in determining nest assessment time is not unequivocal. Indeed experiments in Chapter II showed that transport decisions were made at higher quorum values for familiar than for unfamiliar nest sites; additionally, quorum thresholds were highly correlated with the number of workers present in the familiar nest at the beginning of emigration, and there was no

correlation between either of these variables and assessment time (see p20). Additionally, colonies do not always make decisions at fixed quorum thresholds: quorum values can be lowered in emergency conditions (Franks *et al.* 2003a) or increased for non-urgent emigrations (Dornhaus *et al.* 2004), and may depend on colony size (Dornhaus & Franks 2006; Franks *et al.* 2006a). The relation between quorum sensing and assessment time therefore needs to be investigated in further detail. Possible roles of chemical marking and individual memory should also be considered. There is clear evidence that *Temnothorax* workers lay chemicals on the floors they walk on (Aron *et al.* 1993; Franks *et al.* 2007a) and more specifically inside candidate nest sites (Mallon & Franks 2000; Pratt 2005); chemical marking of candidate sites was also shown to play an important role in nest size assessment (Mallon & Franks 2000; Mugford *et al.* 2001) and to be necessary to ensure continued transport to a chosen nest (Pratt 2005). Pheromones were not reported to have any influence on the type of recruitment (i.e. tandem run or transport) initiated by workers, mainly determined by social interactions within the new nest (Pratt 2005); however, these experiments involved only unfamiliar new nest sites, and the possible influence of chemicals on individual latencies to first transport (i.e. time between discovery of the new site and first transport) and pre-transport evaluation times (i.e. total time spent inside the new site before initiating transport) was not investigated. Similarly, it is uncertain whether informed workers rely at least partly on their memory when evaluating familiar nest sites (see Chapter IV).

The experiments described in the following sections were aimed at determining whether social interactions, chemical cues and individual memory influenced (i) new nest site evaluation and recruitment by informed and/or naïve workers during the assessment phase, i.e. before decisions to initiate transport were made, and (ii) the criterion used by informed and/or naïve workers to switch from evaluation to transport. These two parameters were evaluated by measuring pre-transport approximate rates of population increase and quorum threshold values, respectively. We found that social interactions and quorum sensing alone were not sufficient to account for the lower assessment times observed for familiar good nest sites. Pheromone marking of familiar sites was also found to influence evaluation, even by naïve workers, and informed workers were found to rely at least partly on their private memory during nest assessment. This indicates that both private and social information are used by workers during the assessment of familiar good nest sites, resulting in earlier initiation of transport, which helps to expedite emigrations and/or bias colony preference towards these sites.

METHODS

General methods

A series of five experiments were performed to investigate what type of information workers used when assessing high-quality, familiar nest sites (Table V-1).

Experiment	Treatment	Private information	Chemical marking	Social interactions	
				Workers in	Free access
QT 1 *n = 19*	Control	No	No	No	Yes
	Test	Yes	Yes	No	Yes
QT 2 *n = 18*	Control	Yes	Yes	Yes	Yes
	Test	Yes	Yes	No	Yes
P 1 *n = 18*	Control	Yes	Yes	No	Yes
	Test	Yes	No	No	Yes
P 2 *n = 22*	Control	No	No	No	Yes
	Test	No	Yes	No	Yes
M *n = 16*	Control	No	No	No	No
	Test	Yes	No	No	No

Table V-1 Experimental designs

Experiments were carried out in the geometrically complex arenas described in Chapter II (Figure II.1, see p15). Colonies housed in good nests (see p14) were positioned in the middle of the central dish and allowed to explore the experimental arena for one week. They were then induced to *emigrate to a single good new nest site* identical to their home nest, positioned at one end of the arena.

Webcams connected to motion detection software were used to monitor all activity through the new nest entrance during emigrations (see Chapter II, p17). Analysis of pictures then allowed the monitoring of nest population over time and the determination of *approximate colony-level quorum thresholds* and of *discovery*, *assessment* and *emigration times*, as explained in Chapter II (see p17). Although it fluctuated notably during the assessment period, nest population progressively increased over time until the beginning of transport. In other words, nest population repeatedly reached new maximal values. The *times at which successive new maxima were reached since the discovery of the nest* were recorded until transport started and served as metrics to evaluate the rate of nest population increase.

Colonies displaying little activity during the exploration period and colonies which emigrated to the new nest site were excluded from the final analyses as explained in Chapter II (see p16). For simplicity, the sample sizes mentioned in the following sections and in Table

V-1 correspond to the number of colonies included in the final analyses. In all experiments, every colony was tested once under control and once under test conditions; half of the colonies received the 'control' treatment first, whereas the other half received the 'test' treatment first.

(1) The role of social interactions

Experiments QT1 and QT2 (Table V-1) were performed to investigate whether the faster assessment of familiar good nests observed in Chapter II (see p21) can be fully explained by the quorum threshold being reached earlier in familiar than in unfamiliar nests. In experiment QT1, we tested whether populations increased at similar or different rates, and whether decisions to start carrying were made at similar or different quorum thresholds for familiar and unfamiliar nest sites. In experiment QT2, we tested whether delaying the initial population increase in familiar sites by removing all workers from the nest at the onset of emigration had an impact on nest assessment time.

Experiment QT1

In control conditions, colonies (n = 19) had no available nest site to visit during exploration (*i.e. no private information*). They then emigrated to a single unfamiliar, novel nest site (*i.e. neither chemical marking nor workers inside the nest at emigration onset*). By contrast, in the test, colonies (n = 19) were allowed to familiarise themselves with a high-quality, available nest site during exploration (*i.e. private information*). The familiar nest was then opened by lifting the top glass slide, and all workers present inside the nest were gently removed with soft tweezers and released near the old nest. The familiar nest was then closed back and emigration was induced immediately thereafter (*i.e. chemical marking of the nest but no workers inside the nest at emigration onset*; Table V-1).

Experiment QT2

In both control and test conditions, colonies (n = 18) were allowed to familiarise themselves with a single high-quality, available nest site during exploration (*i.e. private information*). In the test, the familiar nest was then opened by lifting the top glass slide, and all workers present inside the nest were gently removed with soft tweezers and released near the old nest (*i.e. chemical marking but no workers inside the nest at emigration onset*). In the control, the familiar nest was also opened by lifting the top glass slide to induce similar disturbance, but workers were left inside the nest (*i.e. chemical marking and presence of workers inside the nest at emigration onset*). In both treatments, the familiar nest was then closed back and emigration was induced immediately thereafter (Table V-1).

(2) The role of chemical communication

Experiments P1 and P2 (Table V-1) were performed to investigate the effect of nest chemical marking on the assessment time of familiar good nests sites by both 'informed' and 'naïve' colonies (as defined in Chapter II; see p16). In experiment P1, we tested whether removing chemical marking from familiar nest sites had an impact on assessment time by informed colonies. In experiment P2, we tested whether chemical marking laid by informed nestmates had an impact on assessment time by naïve colonies.

Experiment P1

In both control and test conditions, colonies (n = 18) were allowed to familiarise themselves with a single high-quality, available nest site during exploration (*i.e. private information*). In both control and test conditions, the familiar nest was then opened by lifting the top glass slide, and all workers present inside the nest were gently removed with soft tweezers and released near the old nest (*i.e. no workers inside the nest at emigration onset*). In the control, the familiar nest was then closed (*i.e. chemical marking of the nest*) whereas in the test, it was replaced with an identical, fresh nest (*i.e. no chemical marking of the nest*). Emigration was induced immediately thereafter (Table V-1).

Experiment P2

Twenty-two colonies were split into two equal halves (e.g. mother colony Y was split into Y_1 and Y_2). During exploration, 'informed' half-colonies were allowed to familiarise themselves with a single high-quality, available nest site whereas 'naïve' half-colonies had no available nest site to visit (*i.e. no private information*). In the control, naïve half-colonies were then induced to emigrate to a fresh, unfamiliar nest site (*i.e. neither chemical marking nor workers inside the nest at emigration onset*). In the test, familiar nests from informed half-colonies were opened by lifting the top glass and all workers present inside the nest were gently removed. The nest was then closed back and transferred to naïve half-colonies (*i.e. chemical marking but no workers inside the nest at emigration onset*). Naïve half-colonies were then immediately induced to emigrate to the transferred nest. To avoid any confounding effects of nestmate recognition (Franks *et al.* 2007a), transfers were always done between half-colonies from the same mother colony, as they usually share the same colony odour during several weeks in *Temnothorax* sp. (Stroeymeyt *et al.* 2007).

(3) The role of memory

Experiment M was performed to investigate whether workers have private information stored in their memory about the suitability of good familiar nest sites. The experimental design therefore aimed at (i) removing all (both private and public) chemical marking of the new nest, and (ii) strictly controlling social interactions within the new nest, so that individual memory was the only parameter distinguishing test from control treatments (Table V-1).

All workers in 16 colonies (range: 70-165, median 117 workers per colony) were individually marked with paint as described in Chapter IV (see p56).

In control conditions, colonies had no available nest site to visit during exploration (*i.e. no private information*). They then emigrated to a single unfamiliar, novel nest site (*i.e. neither chemical marking nor workers inside the nest at emigration onset*). By contrast, in the test, colonies were allowed to familiarise themselves with a single high-quality, available nest site during exploration (*i.e. private information*). The familiar nest was then replaced with an identical, fresh nest site and emigration was induced immediately thereafter (*i.e. neither chemical marking nor workers inside the nest at emigration onset*; Table V-1).

During emigrations, vertically sliding acetate doors fitted through the tunnels leading to the new nest site (Figure V.4) were used to control access of ants to the new site for both test and control colonies (*i.e. no free access to the new nest*). At the beginning of emigration, the sliding doors were open and allowed free passage to and from the peripheral dish containing the new nest. As soon as the new nest was entered by the first worker (‘first discoverer’), the doors were closed down and any other worker remaining in the peripheral dish was gently removed with soft tweezers and released near the old nest. Sliding doors were then manually opened and closed so as to allow free passage to the first discoverer, but to no other worker. After the first discoverer started to recruit nestmates to the new site (either by tandem running or by transport), free passage was allowed to the first discoverer and to all successively recruited ants, but to no other worker. Access control and data recording were carried out until a total of 20 workers had been recruited to the new nest. If the first discoverer failed to recruit nestmates within 90 minutes of nest discovery, the new nest was replaced by an identical, fresh new nest. The next worker was allowed inside the new site and the experiment proceeded as explained above.

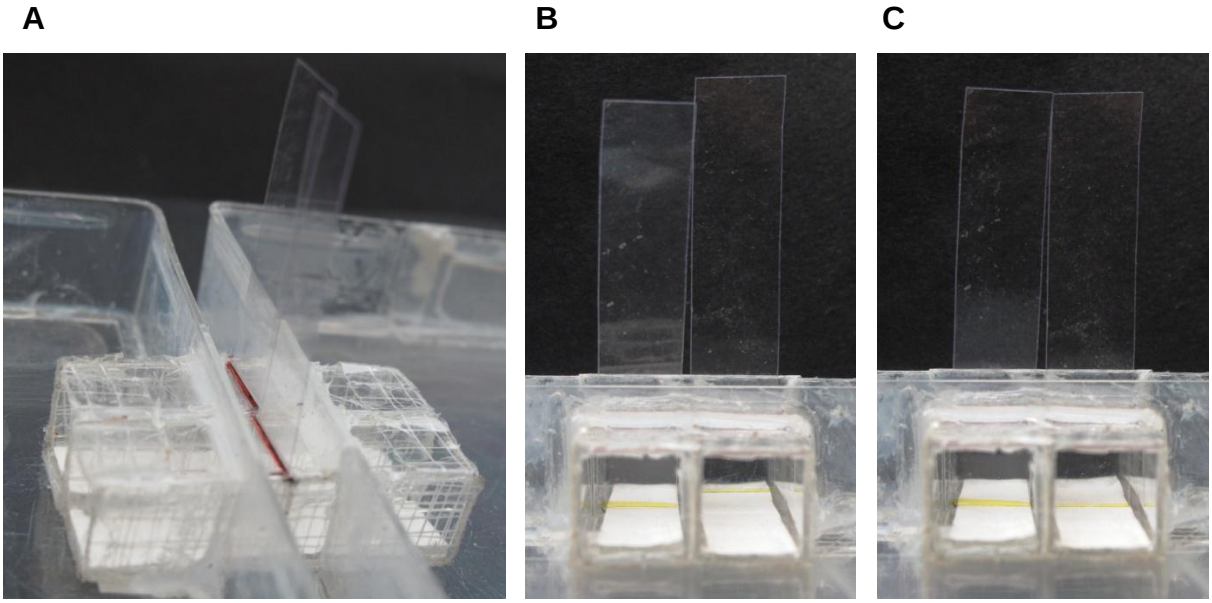

Figure V.4 Acetate sliding doors
Perspective view **(A)** and front views **(B-C)** of two tunnels fitted with acetate sliding doors. Sliding doors were introduced through a top slit cut in the middle of the tunnels **(A)** and were lifted or dropped manually to allow or prevent passage. The right hand side door is shown open **(B)** or closed **(C)**.

Data recording and analysis was performed for as described above (see p86). Additionally, the *total numbers of attempted and successful tandem runs* led to the new nest were recorded (tandem runs were considered successful when they reached the peripheral dish containing the new nest site; attempted tandem runs included both successful and interrupted tandem runs). Individual data was also collected for first discoverers and for all workers that recruited nestmates to the new site during the recording period. Individual *first recruitment decisions* (tandem running, transport or – for first discoverers– no recruitment) were recorded. Additionally, the *latency to tandem running* (i.e. time interval between the first entrance in the new site and the first tandem run), the *timing and duration of all visits* to the new nest before the first tandem run and the *number of successful tandem runs* led were recorded for every tandem leader. Finally, the *latency to transport* (i.e. time interval between the first entrance in the new site and the first transport act), the *timing and duration of all visits* to the new nest before the first transport act, the *number of successful tandem runs* led, and the *individual quorum threshold* used (i.e. maximum number of workers present inside the nest during the visit directly preceding the first transport act) were recorded for every transporter. This then allowed the calculation for each recruiter of pre-tandem and pre-transport *individual evaluation time* (total duration spent inside the new nest site before the first tandem run or before the first transport act), *total number of visits* and *average visit time* (calculated by dividing the evaluation time by the number of visits).

Statistical analyses

In all experiments, colony-level emigration variables were compared among treatments using SPSS general linear mixed model procedure (GLMM) with fixed factor 'Treatment' (test vs. control) and random factors 'Colony' and 'Block'.

To compare the rate of increase of the nest population among treatments, the variable 'New population maximum' was analysed using a GLMM procedure with fixed factor 'New nest site', covariate 'Time since first discovery' and its interaction with 'Treatment', and random factors 'Colony' and 'Blocks'. The analysis was not performed for experiment QT2 because of the different initial conditions between test and control conditions: in the test all workers were gently removed from the familiar nest at the onset of emigration and released near the old nest, whereas in the control, they were left inside the nest. This manipulation was likely to have a strong impact on the rate of increase in nest population, simply because the pool of informed workers outside of the familiar nest (and therefore the number of potential informed discoverers) was artificially increased in the test. No meaningful comparisons could therefore be done between test and control colonies.

In experiment M, individual-level variables concerning tandem running by first discoverers were compared among treatments using a GLMM with fixed factor 'Treatment' (naïve vs. unfamiliar) and random factors 'Colony' and 'Block'. Individual-level variables concerning transport by first discoverers were compared using a similar GLMM procedure with an additional fixed factor, i.e. 'First recruitment decision' (transport vs. tandem run) and its interaction with 'Treatment'. Individual-level variables concerning all recruiters were analysed with similar GLMM procedures with another additional fixed factor, i.e. 'Rank of entrance into the new nest', and its interaction with 'Treatment'.

For all GLMM procedures we selected the model fitting our data best by using a stepwise backward procedure. Statistical significance was tested using an Analysis of Deviance with a Type III Sum of Squares method (comparison of the full model to the full model without the factor of interest). Normality and homoscedasticity of residuals were checked using Kolmogorov-Smirnov and Levene's tests. If residuals were not normally distributed, we applied either log- or power-transformation to the data. In cases where we could not identify any transformation allowing normalisation of residuals, we used other parametric or non-parametric tests. We then used paired tests for colony-level variables (Wilcoxon matched-pairs tests). By contrast, tests on individual-level variables were unpaired (unpaired t-tests or Mann-Whitney U-tests), because the individuals involved were all different.

Finally, in experiment M, first recruitment decisions among first discoverers or among all recruiters were compared between treatments using Fisher-Freeman-Halton's (first discoverers; transport vs. tandem run vs. no recruitment; Freeman & Halton 1951; Weisstein 2010) or Fisher's exact tests (all recruiters; transport vs. tandem run).

RESULTS

Nest visits

A grand total of 5457 visits – corresponding to 186 emigrations – were analysed over five experiments (QT1: n = 666; QT2: n = 636; P1: n = 852; P2: n = 727; M: n = 2576).

(1) The role of social interactions

Experiment QT1

Colonies emigrating to a familiar nest (test) were faster than colonies emigrating to an unfamiliar nest (control), even though the familiar nest had been emptied of workers at the beginning (Figure V.5 A; GLMM, effect of treatment, $F_{1,14} = 25.233$, $p < 0.001$). Additionally, workers led significantly fewer tandem runs to familiar than to unfamiliar nest sites (GLMM, effect of treatment, $F_{1,14} = 10.834$, $p < 0.005$). Finally, assessment time (i.e. time interval between first discovery of the new nest and full commitment to that nest) was lower and the quorum threshold reached earlier for familiar than in unfamiliar nests (Figure V.5 A; GLMM, effect of treatment, $F_{1,14} \geq 35.851$, $p < 0.001$ in both cases).

These observations could at least partly be explained by the faster population increase recorded in familiar than in unfamiliar sites (Figure V.5 B; GLMM, interaction treatment x time: $F_{1,117} = 10.669$, $p < 0.001$). However, the rate of population increase was not the only factor responsible for the quicker assessment of familiar nest sites. Indeed, this was also due to decisions to start carrying being made at significantly lower quorum thresholds for familiar than for unfamiliar sites (Figure V.5 A; GLMM, effect of treatment, $F_{1,14} = 5.695$, $p < 0.05$).

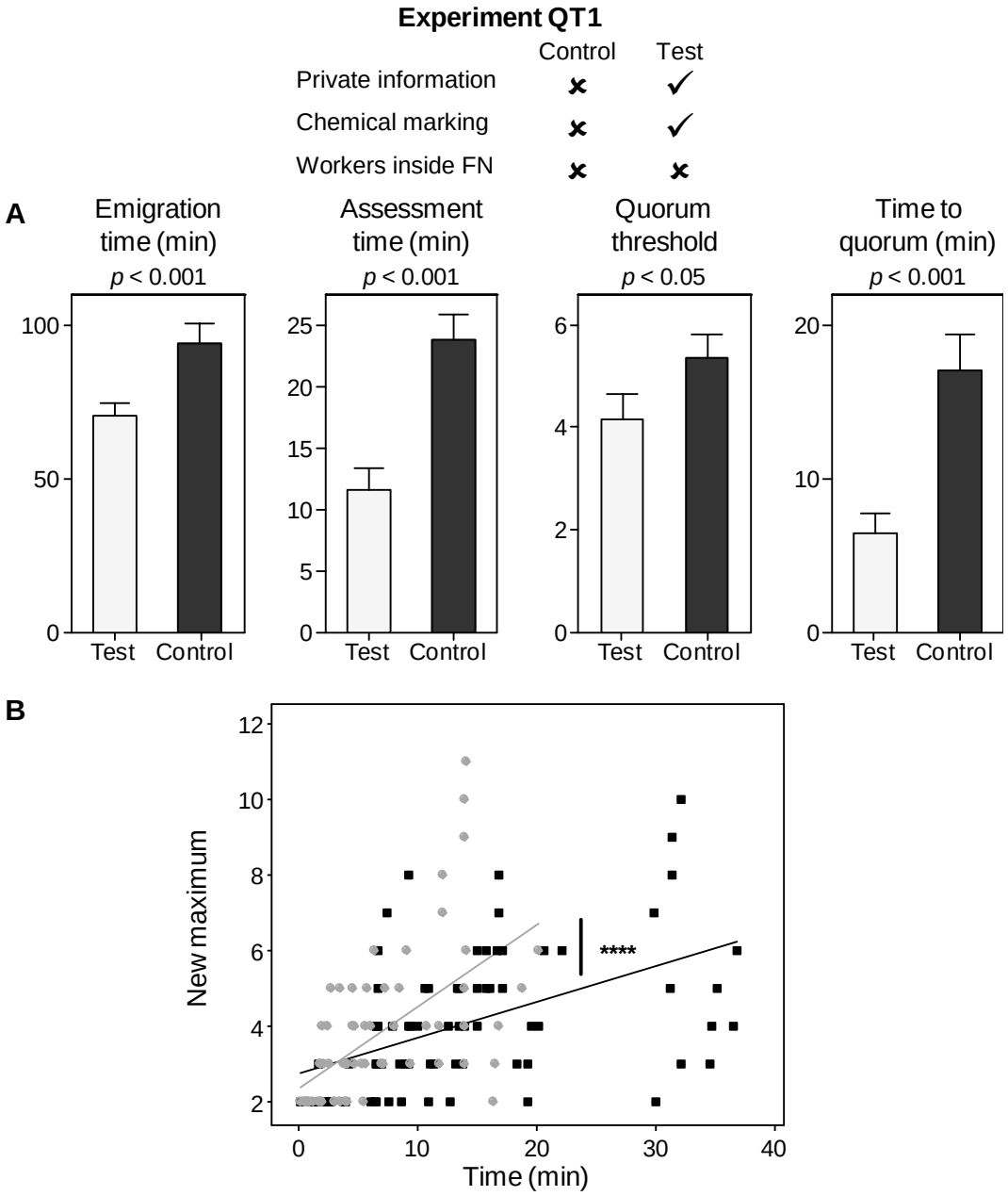

Figure V.5 Experiment QT1
(A) Emigration time, assessment time, quorum threshold and time to reach the quorum threshold for test (light grey) and control (dark grey) colonies (n = 19) emigrating to a single, high-quality new nest site (emigration characteristics in test and control conditions are summarised in the top table). Bars and whiskers represent means and standard errors, respectively. *P*-values are given for the effect of treatment on all variables (GLMM; no data transformation). **(B)** New population maxima as a function of time after nest discovery for test (grey circles and line) and control (black squares and line). GLMM analysis with colony and block as random factors showed a significant interaction between time and treatment (********: $F_{1,117} = 10.669$, $p < 0.001$).

Experiment QT2

Control and test colonies emigrating to familiar nest sites showed no differences in overall emigration times, even though the nest had been emptied of workers at the beginning for test colonies (Figure V.6; GLMM, effect of treatment, $F_{1,12} = 0.731$, $p = 0.41$). Additionally, workers led similar numbers of tandem runs to the familiar and to the unfamiliar nest site (Wilcoxon matched-pairs test, Z = -0.632, n = 18, $p = 0.53$). Assessment times did not differ and quorum thresholds were reached at similar times in the control and the test (Figure V.6; GLMM, effect of treatment, assessment time: $F_{1,12} = 0.009$, $p = 0.93$; time to reach quorum: $F_{1,12} = 0.022$, $p = 0.88$). Interestingly, however, decisions to start carrying were made at significantly lower quorum thresholds in test than in control conditions, due to the initial worker depletion in test colonies (Figure V.6; GLMM, effect of treatment, $F_{1,12} = 6.183$, $p < 0.05$).

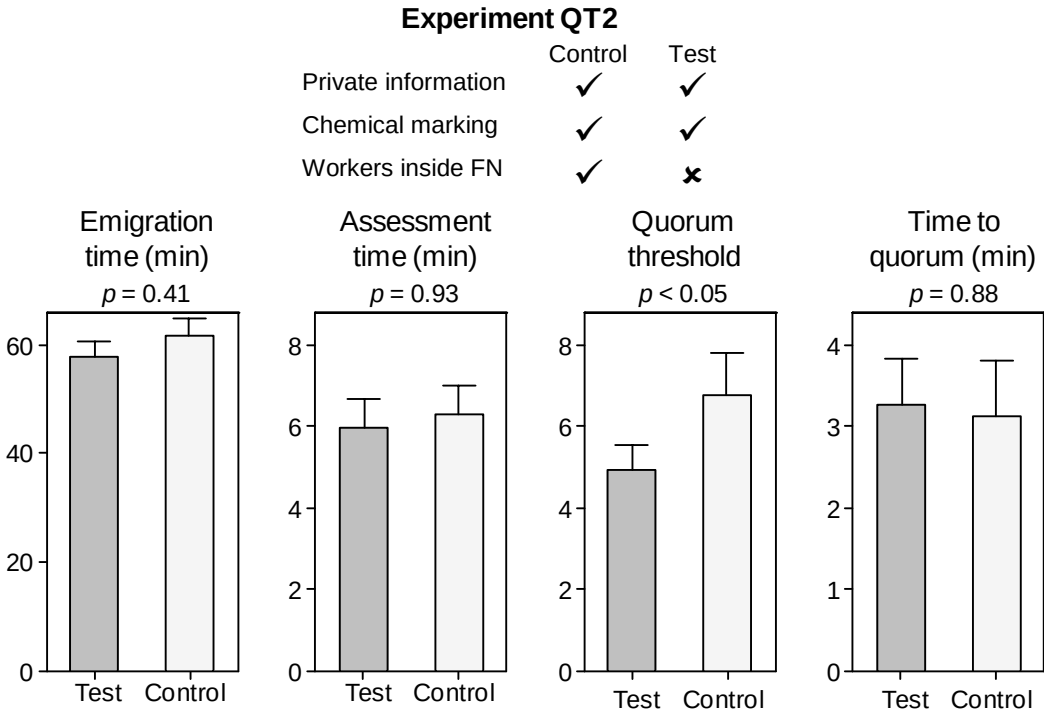

Figure V.6 Experiment QT2
Emigration time, assessment time, quorum threshold and time to reach the quorum threshold for test (dark grey) and control (light grey) colonies (n = 18) emigrating to a single, high-quality new nest site (emigration characteristics in test and control conditions are summarised in the top table). Bars and whiskers represent means and standard errors, respectively. *P*-values are given for the effect of treatment on all variables (GLMM; no data transformation).

Taken together, the results of experiments QT1 and QT2 strongly suggest that social interactions and quorum sensing are not the only determinants of full commitment to a new nest site. Indeed quorum threshold values were different for familiar and unfamiliar nest sites, and also differed for identical familiar nest sites depending on initial population conditions. This shows that nest assessment time does not solely reflect the time necessary for the nest population to reach a given, fixed quorum threshold. Social interactions are therefore not sufficient to explain the faster assessment of familiar nest sites, and other factors are likely to play a role in recruitment decisions by workers.

(2) The role of chemical communication

Experiment P1

Colonies emigrating to familiar nests initially emptied of workers showed no differences in overall emigration time whether chemical marking of the nest had been left (control) or removed (test; Figure V.7 A; GLMM, effect of treatment, $F_{1,11} = 0.826$, $p = 0.38$). Additionally, workers led similar numbers of tandem runs to the familiar and to the unfamiliar nest site (Wilcoxon matched-pairs test, Z = -1.354, n = 18, $p = 0.18$). Decisions to start carrying were made at similar quorum thresholds in test and control conditions (Figure V.7 A; GLMM, effect of treatment, $F_{1,12} = 0.775$, $p = 0.40$), but the quorum threshold was reached significantly later and nest assessment tended to take longer when chemical marks had been removed (Figure V.7 A; time to reach quorum, GLMM, effect of treatment: $F_{1,12} = 5.748$, $p < 0.05$; assessment time, paired t-test: t = -2.017, df = 17, $p = 0.06$). This was mainly due to the faster increase in nest population observed when chemical marking of the familiar was left untouched than when it was removed (Figure V.7 B; GLMM, interaction treatment x time, $F_{1,150} = 6.569$, $p < 0.05$).

These results indicate that chemical marking of the familiar nest contributes to faster assessment of that nest in later emigrations by informed colonies. However, it is still unclear whether these chemical marks are only informative to the workers that laid them or whether they convey information that naïve nestmates can also use.

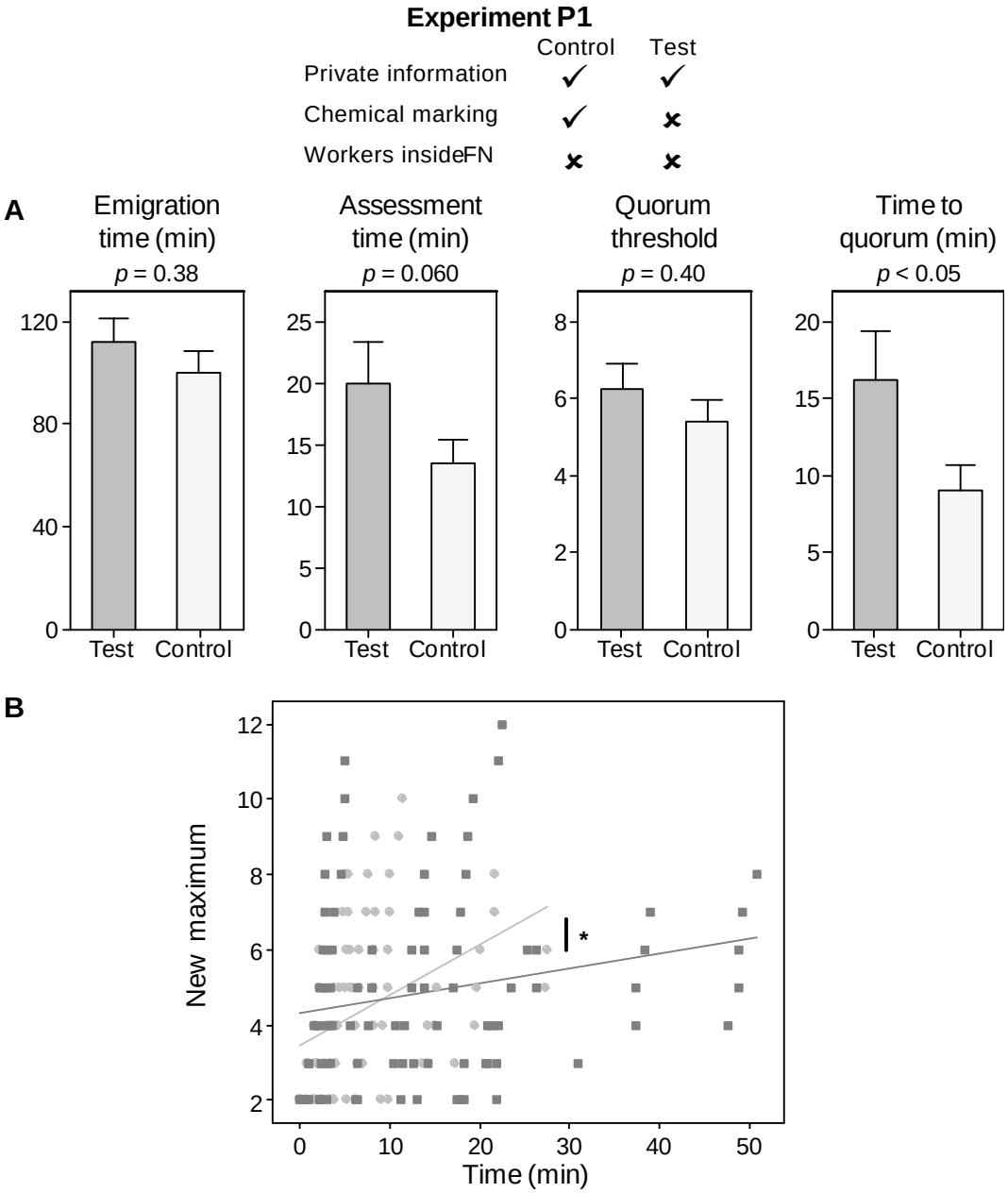

Figure V.7 Experiment P1
(A) Emigration time, assessment time, quorum threshold and time to reach the quorum threshold for test (dark grey) and control (light grey) colonies (n = 18) emigrating to a single, high-quality new nest site (emigration characteristics in test and control conditions are summarised in the top table). Bars and whiskers represent means and standard errors, respectively. *P*-values are given for the effect of treatment on all variables (GLMM or paired t-test; no data transformation). **(B)** New population maxima as a function of time after nest discovery for test (dark grey squares and line) and control (light grey circles and line). GLMM analysis with colony and block as random factors showed a significant interaction between time and treatment (*****:$F_{1,150} = 6.569$, $p < 0.05$).

Experiment P2

Naïve half-colonies emigrating to unfamiliar nest sites that had been previously visited by nestmates (test) tended to be faster than naïve half-colonies emigrating to fresh, previously unvisited unfamiliar nest sites (control; Figure V.8 A; GLMM, effect of treatment: $F_{1,9}$ = 4.852, p = 0.055). This was partly due to nest assessment time being significantly lower in test than in control conditions (Figure V.8 A; GLMM, effect of treatment: $F_{1,9}$ = 5.439, p < 0.05). Workers led similar numbers of tandem runs to the familiar and to the unfamiliar nest site (GLMM, effect of treatment: $F_{1,9}$ = 0.948, p = 0.36). Additionally, decisions to start carrying were made for similar quorum thresholds in the control and in the test (Figure V.8 A; GLMM, effect of treatment: $F_{1,9}$ = 1.720, p = 0.22). The observed faster assessment in test conditions was therefore mainly due to the earlier increase in population recorded in the test (Figure V.8 B; population increased at similar rates in the test and the control, but was generally higher in the test than in the control for any given time: GLMM, interaction treatment x time: $F_{1,89}$ = 0.475, p = 0.49; effect of treatment, $F_{1,90}$ = 10.541, p < 0.005). This resulted in the quorum threshold being reached slightly earlier in the test, although this trend was not statistically significant (Figure V.8 A; GLMM, effect of treatment: $F_{1,9}$ = 3.465, p = 0.096).

Overall, these results indicate that chemical substances marking the familiar nest influence nest assessment by both informed and naïve workers in later emigrations, and can therefore be considered as pheromones. The effect of chemicals on assessment and overall emigration times was stronger in naïve than in informed colonies, suggesting that informed workers may also use other sources of (private) information while assessing the nest.

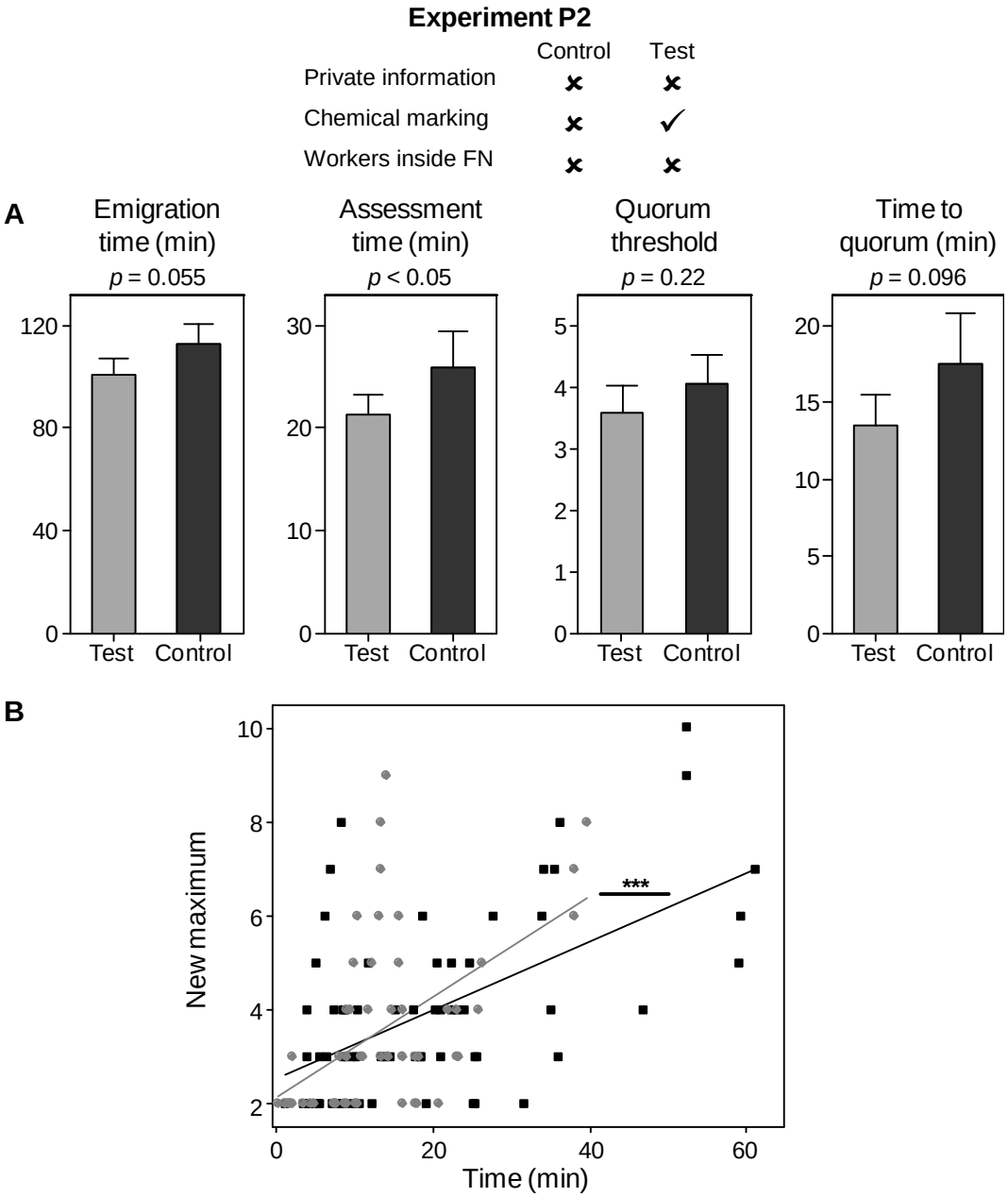

Figure V.8 Experiment P2
(A) Emigration time, assessment time, quorum threshold and time to reach the quorum threshold for test (light grey) and control (dark grey) naïve colonies (n = 22) emigrating to a single, high-quality new nest site (emigration characteristics in test and control conditions are summarised in the top table). Bars and whiskers represent means and standard errors, respectively. *P*-values are given for the effect of treatment on all variables (GLMM; assessment time, quorum threshold and time to reach quorum threshold were powered-transformed). **(B)** New population maxima as a function of time after nest discovery for test (grey circles and lines) and control (black squares and line). GLMM analysis with colony and block as random factors showed a significant effect of time ($F_{1,90}$ = 114.484, p < 0.001) and of treatment (*******:$F_{1,90}$ = 10.541, p < 0.005).

(3) The role of memory

Colony-level emigration data

Colonies emigrating to a familiar nest (informed) tended to discover the new nest earlier and assessed it significantly faster than colonies emigrating to an unfamiliar nest (naïve; Figure V.9 A; GLMM, effect of treatment, discovery time: $F_{1,15} = 4.289$, $p = 0.056$; assessment time: $F_{1,15} = 10.822$, $p < 0.005$). Additionally, fewer successful and attempted tandem runs were led to familiar than to unfamiliar nest sites (Figure V.9 B; GLMM, effect of treatment, attempted tandem runs: $F_{1,14} = 5.570$, $p < 0.05$; successful tandem runs: $F_{1,14} = 4.554$, $p = 0.051$). Finally, decisions to start carrying were made at lower quorum thresholds for familiar than unfamiliar nest sites (Figure V.9 C; GLMM, effect of treatment: $F_{1,14} = 12.510$, $p < 0.005$). These results are in agreement with those presented in Chapter II (see p19). This confirms that informed colonies had gathered information about familiar nest sites during exploration, and shows that they were able to use that information during emigrations even though nest marking pheromones had been removed and social interactions were restricted to a minimum.

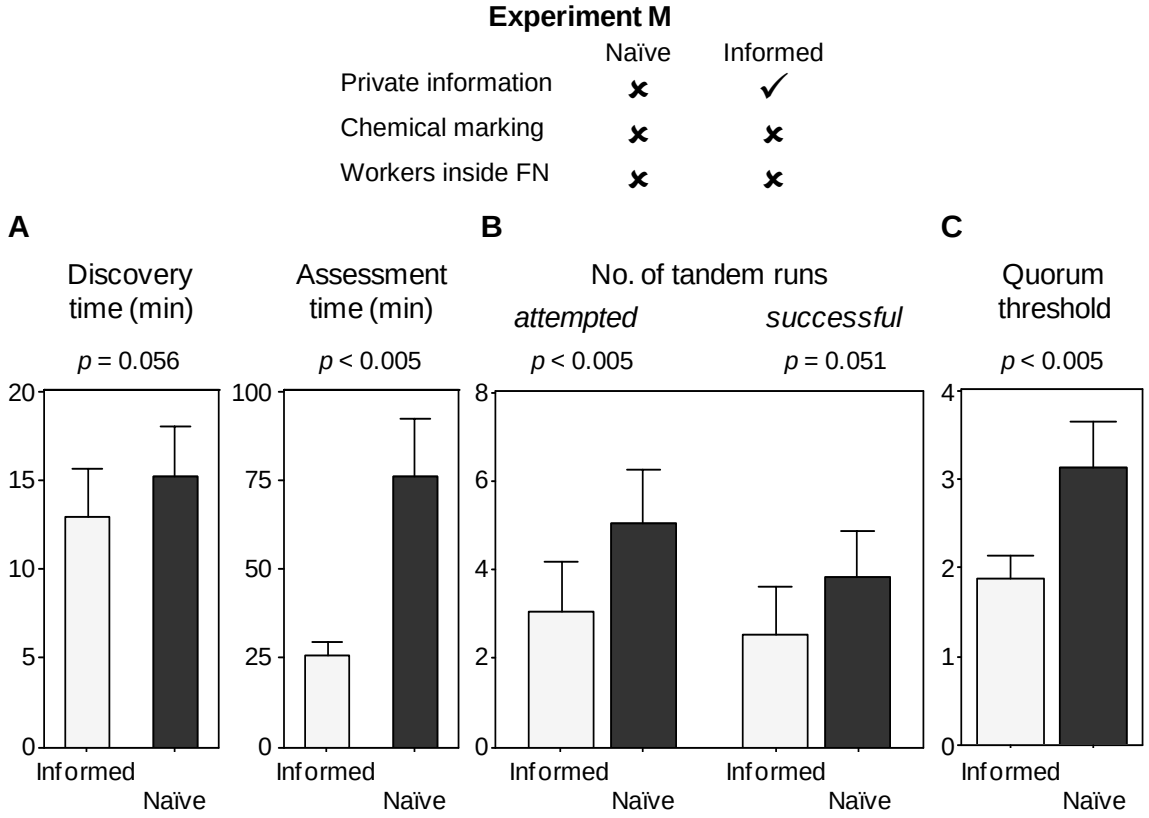

Figure V.9 Colony-level emigration data
(A) Discovery and assessment times, **(B)** number of attempted and successful forward tandem runs and **(C)** quorum threshold for informed (light grey) and naïve (dark grey) colonies (n = 16) emigrating to a single, high-quality new nest site (emigration characteristics are summarised in the top table for informed and naïve colonies). Bars and whiskers represent means and standard errors, respectively. *P*-values are given for the effect of treatment on all variables (GLMM; discovery time was power-transformed).

First recruitment decisions

Over all emigrations (n = 32), 38 first discoverers (informed colonies: n = 16; naïve colonies: n = 22) and 168 recruiters (informed colonies: n = 84; naïve colonies: n = 84) were identified. Informed and naïve colonies differed significantly in the first recruitment decisions made by first discoverers (Figure V.10; Fisher-Freeman-Halton's exact test: $p < 0.05$). More precisely, all first discoverers in informed colonies (n = 16) recruited nestmates to the new site, whereas 6 out of the 22 first discoverers in naïve colonies did not recruit any nestmates to the new site. Additionally, the proportion of first discoverers that initiated recruitment by carrying rather than by tandem running was higher for informed (6 out of 16) than for naïve colonies (2 out of 16). Carrying, tandem running and no recruitment respectively reflect full commitment, partial commitment and no commitment to a nest site (Pratt 2005; Pratt *et al.* 2002; Pratt *et al.* 2005). These results indicate that the initial commitment of first discoverers to the new site was stronger in informed than in naïve colonies, even though there were no nest marking pheromones and there were no other worker inside the nest at that time. This strongly suggests that individual memory plays a role in determining initial commitment of informed workers to the familiar nest.

Informed and naïve colonies also differed significantly in the first recruitment decisions made by all recruiters; more precisely, a higher proportion of recruiters initiated recruitment by carrying rather than by tandem running in informed colonies (Figure V.10; Fisher's exact test: $p < 0.05$). This shows that commitment to the new site was stronger overall in informed than in naïve colonies throughout the recording period.

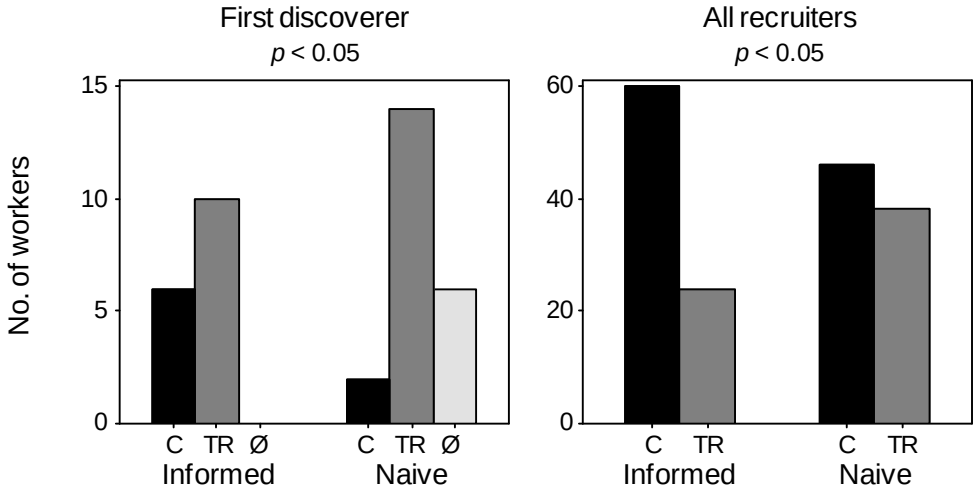

Figure V.10 First recruitment decision
First recruitment decision by first discoverers (left) and by all observed recruiters (right). Bars represent the total number of workers (pooled across colonies) that took a given decision for their first recruitment act (black, C: carrying; dark grey, TR: tandem running; light grey, Ø: no recruitment within 90 min of nest discovery). Data is given separately for informed and naïve colonies. First decision patterns were compared between treatments using Fisher-Freeman-Halton's exact test (first discoverers) or Fisher's exact test (all recruiters).

Recruitment by tandem running

Over all emigrations, 24 out of the 38 first discoverers (informed colonies: n = 10; naïve colonies: n = 14) and 62 out of the 168 recruiters (informed colonies: n = 24; naïve colonies: n = 38) led tandem runs.

Individual latencies to first tandem runs and pre-tandem nest evaluation times were similar for workers from informed and naïve colonies (Leaders among first discoverers: Figure V.11 A; unpaired t-tests, Latency: t = 0.505, df = 22, $p = 0.62$; Evaluation time: t = 0.368, df = 21, $p = 0.72$; All tandem leaders: Figure V.12 A; GLMM, Latency: $F_{1,44} = 1.781$, $p = 0.19$; Evaluation time: $F_{1,41} = 0.466$, $p = 0.50$).

The number of visits and average visit time for each leader before their first tandem run did not differ for informed and naïve colonies (Leaders among first discoverers: Figure V.11 B; Mann-Whitney U-tests, No. of visits: U = 55.0, $p = 0.35$; Average visit time: U = 59.5, $p = 0.74$; All tandem leaders: Figure V.12 B; GLMM, No. of visits: $F_{1,43} = 0.326$, $p = 0.57$; Average visit time: $F_{1,43} = 3.125$, $p = 0.08$).

Finally, tandem leaders led similar numbers of tandem runs to the new site in informed and naïve colonies. In both treatments the number of tandem runs per leader depended strongly on the rank of entrance into the new nest, i.e. workers that entered the nest earlier tended to lead more tandem runs (Leaders among first discoverers: Figure V.11 C; Mann-Whitney U-test, U = 55.5, $p = 0.39$; All tandem leaders: Figure V.12 C; GLMM, effects of treatment: $F_{1,43} = 0.038$, $p = 0.85$; entrance rank: $F_{1,43} = 31.413$, $p < 0.001$).

These results indicate that individuals that made the decision to recruit nestmates to the new site via tandem running behaved in a similar way in informed and naïve colonies, both during the pre-tandem evaluation period and in their recruitment activity.

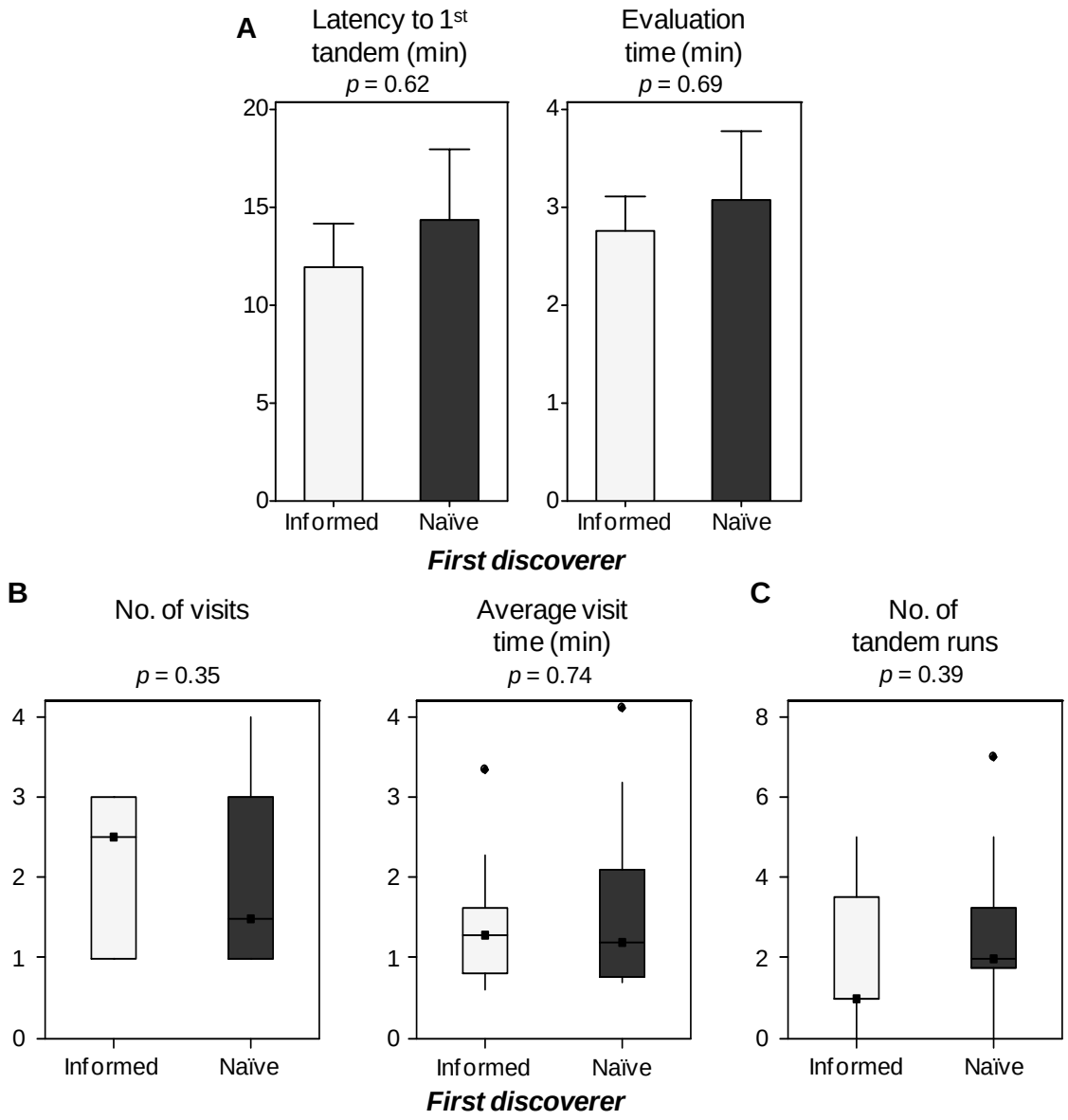

Figure V.11 Tandem running by first discoverers
(A) Latency to first tandem running and pre-tandem evaluation time for first discoverers that led tandem runs in informed (light grey, n = 10) and naïve (dark grey, n = 14) colonies. Bars and whiskers represent means and standard errors, respectively. *P*-values are given for the effect of treatment on both variables (unpaired t-tests; Normality of data, Kolmogorov-Smirnov tests, Latency: Informed, KS = 0.206, df = 10, $p > 0.2$; Naïve, KS = 0.213, df = 14, $p = 0.085$; Evaluation time: Informed, KS = 0.134, df = 10, $p > 0.2$; Naïve, KS = 0.222, df = 14, $p = 0.078$; Equality of variances, F test, Latency: $F_{9,13} = 1.821$, $p = 0.19$; Evaluation time: $F_{9,13} = 4.710$, $p = 0.042$, hence equal variances not assumed to perform the test). **(B)** Total number of visits and average visit time before the first tandem run, and **(C)** total number of successful forward tandem runs for first discoverers that led tandem runs in informed (light grey) and naïve (dark grey) colonies (Mann-Whitney U-tests, No. of visits: U = 55, Z = -0.935, $p = 0.35$; Average visit time: U = 59.5, Z = -0.341, $p = 0.74$; No. of tandem runs: U = 55.5, Z = -0.869, $p = 0.39$). Full squares, rectangles, whiskers and circles represent the median, interquartile range, 1.5 x interquartile range and outliers, respectively.

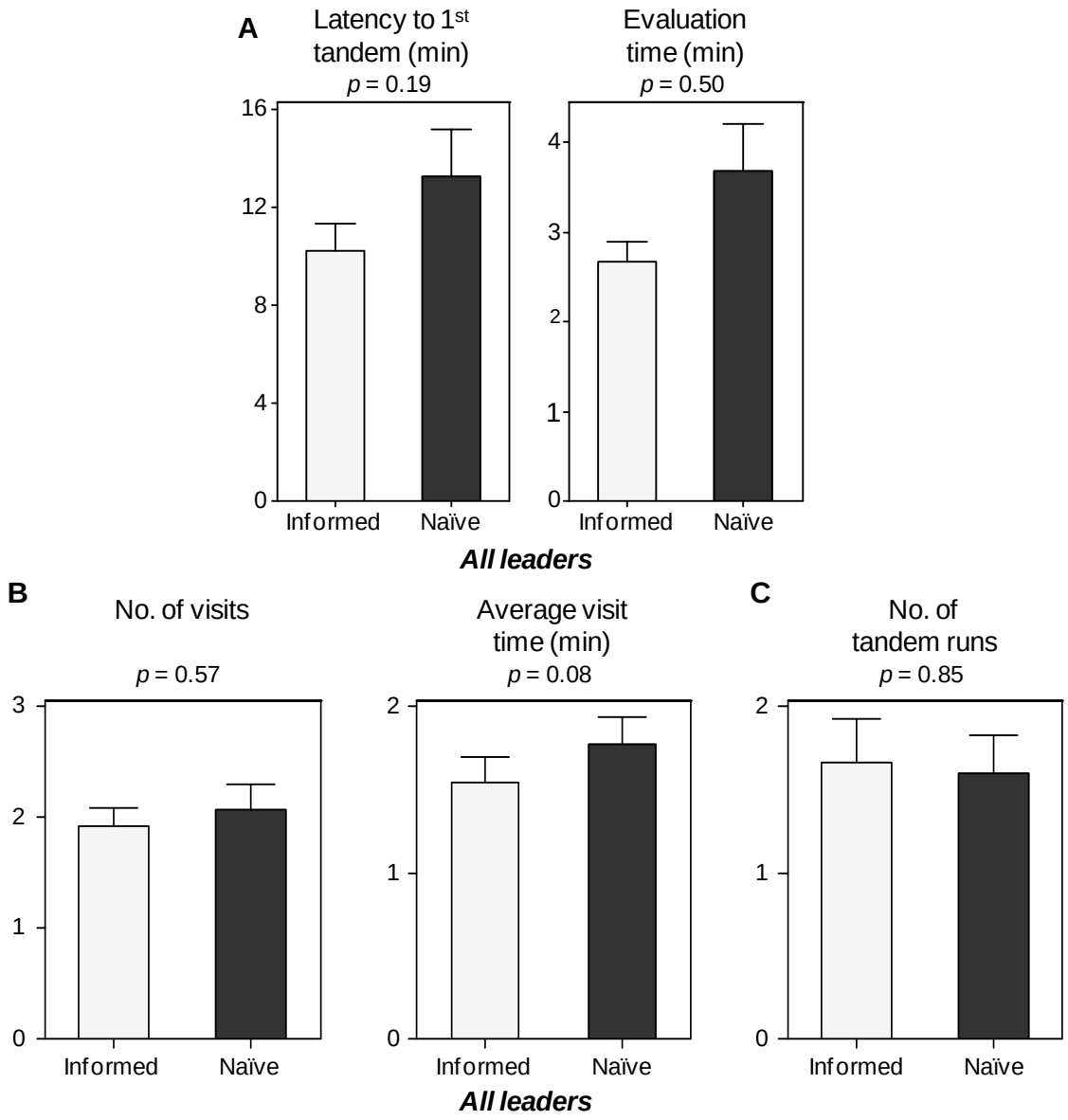

Figure V.12 Tandem running by all leaders
(A) Latency to first tandem running and pre-tandem evaluation time; **(B)** total number of visits and average visit time before the first tandem run; and **(C)** total number of successful forward tandem runs for all tandem leaders in informed (light grey, n = 24) and naïve (dark grey, n = 38) colonies. Bars and whiskers represent means and standard errors, respectively. *P*-values are given for the effect of treatment on all variables (GLMM; Latency, Evaluation time and No. of visits were Log-transformed).

Transport

Over all emigrations, 32 out of the 38 first discoverers (informed colonies: n = 16; naïve colonies: n = 16) and 149 out of the 168 recruiters (informed colonies: n = 72; naïve colonies: n = 77) carried nestmates to the new site.

Individual latencies to first transport and pre-transport nest evaluation times were significantly lower for workers from informed than from naïve colonies. Additionally, they became shorter as the rank of entrance into the new nest increased (Transporters among first discoverers: Figure V.13 A; GLMM, Latency: effect of treatment, $F_{1,14} = 7.406$, $p < 0.05$; Evaluation time: effect of treatment, $F_{1,14} = 5.416$, $p < 0.05$; All transporters: Figure V.14 A; GLMM, Latency: effect of treatment, $F_{1,128} = 13.206$, $p < 0.001$; effect of entrance rank, $F_{1,128} = 88.133$, $p < 0.001$; Evaluation time: effect of treatment, $F_{1,124} = 5.245$, $p < 0.05$; effect of entrance rank, $F_{1,124} = 16.749$, $p < 0.001$).

Among first discoverers, the faster evaluation in informed colonies was mainly due to individuals making fewer visits to the new nest before initiating transport in informed than in naïve colonies (Figure V.13 B; GLMM, No. of visits: $F_{1,13} = 25.472$, $p < 0.001$; Average visit time: $F_{1,14} = 2.984$, $p = 0.11$). Among all transporters, a similar trend was observed, but it was not significant (Figure V.14 B; GLMM, No. of visits: $F_{1,127} = 2.860$, $p = 0.09$; Average visit time: $F_{1,123} = 2.089$, $p = 0.15$). By contrast, the total number of visits and average visit time before transport depended on the rank of entrance into the new site (GLMM, No. of visits: decrease, $F_{1,127} = 93.600$, $p < 0.001$; Average visit time: increase, $F_{1,123} = 3.846$, $p = 0.052$).

Transporters overall led fewer tandem runs before starting to carry in informed than in naïve colonies (Transporters among first discoverers: Figure V.13 B; GLMM, $F_{1,15} = 12.600$, $p < 0.005$; all transporters: Figure V.14 B; GLMM, $F_{1,127} = 10.953$, $p < 0.001$).

Finally, among first discoverers, transporters made the decision to start carrying at lower quorum thresholds in informed than in naïve colonies (Figure V.13 B; GLMM, $F_{1,14} = 9.242$, $p < 0.01$). When considering all transporters, there were no differences in the individual quorum thresholds used by workers in informed and naïve colonies; quorum values however increased strongly as the rank of entrance into the new nest increased (Figure V.14 B; GLMM, effect of treatment, $F_{1,124} = 2.251$, $p = 0.14$; effect of entrance rank, $F_{1,124} = 92.214$, $p < 0.001$).

Altogether, these results show that before their first transport act (i.e. while they were evaluating the new nest), the behaviour of individual transporters differed between informed and naïve colonies. Workers from colonies that had previously familiarised themselves with the new nest made the decision to start carrying earlier than workers from naïve colonies, and generally led fewer tandem runs. When considering only the first discoverers, it also

appeared that transport decisions were made after fewer visits to the new site and at lower quorum thresholds by individuals from informed than naïve colonies. This was the case even though all chemical marks had been removed from the new site and social interactions were restricted to a minimum. This strongly suggests that individual memory played an important role in decisions by informed workers to launch transport to the familiar nest site. The role of memory appeared to be of particular importance among first discoverers, i.e. in the early steps of emigration, when there were no social interactions among workers. During later stages, when there were several workers inside the new nest and some interactions could therefore occur, memory appeared to play a less important role.

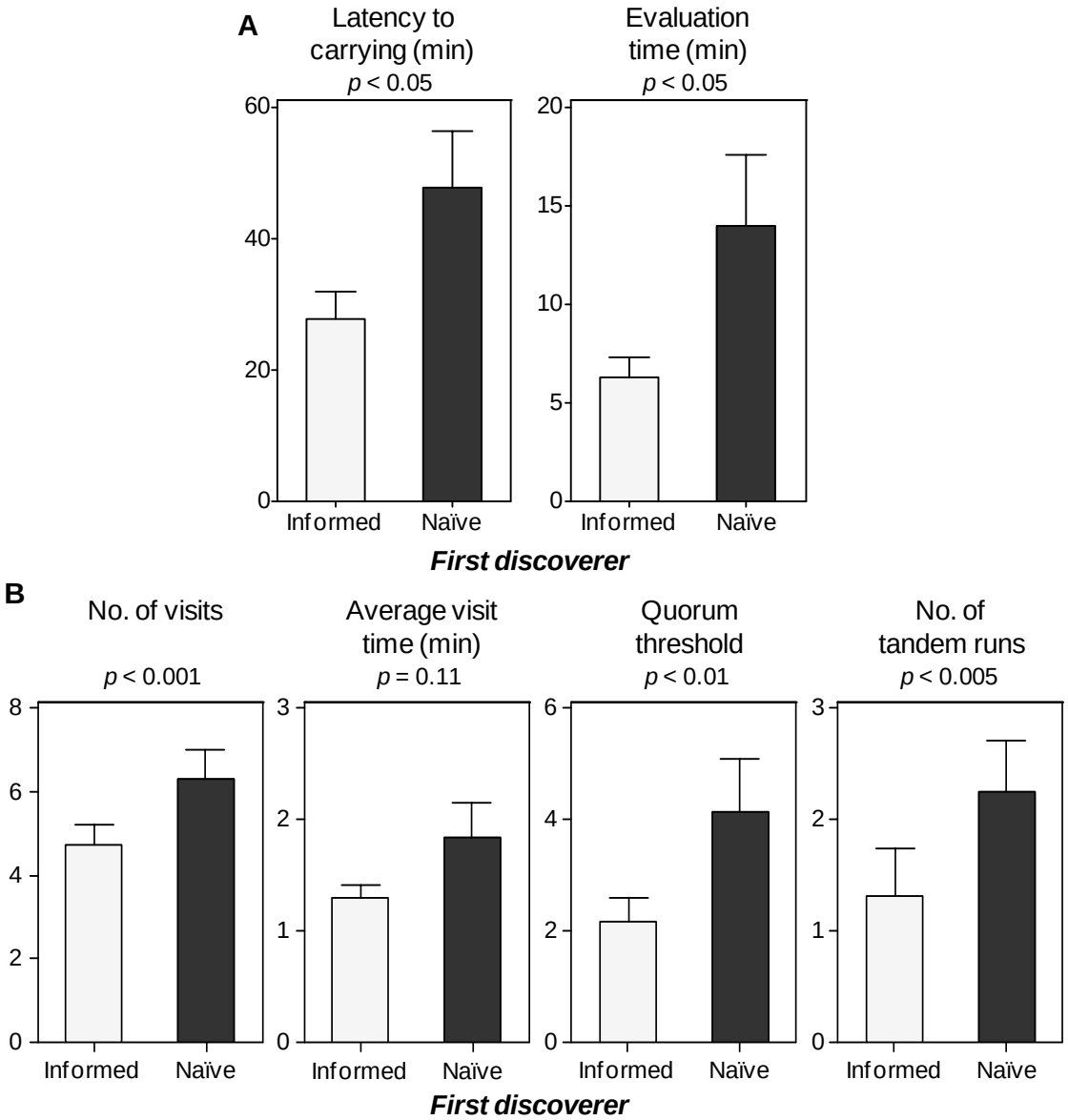

Figure V.13 Transport by first discoverers
(A) Latency to first transport and pre-transport evaluation time; **(B)** total number of visits, average visit time, quorum threshold and total number of tandem runs led before the first transport for first discoverers that were involved in transport in informed (light grey) and naïve (dark grey) colonies. Bars and whiskers represent means and standard errors, respectively. *P*-values are given for the effect of treatment on all variables (GLMM; Average visit time was Log-transformed).

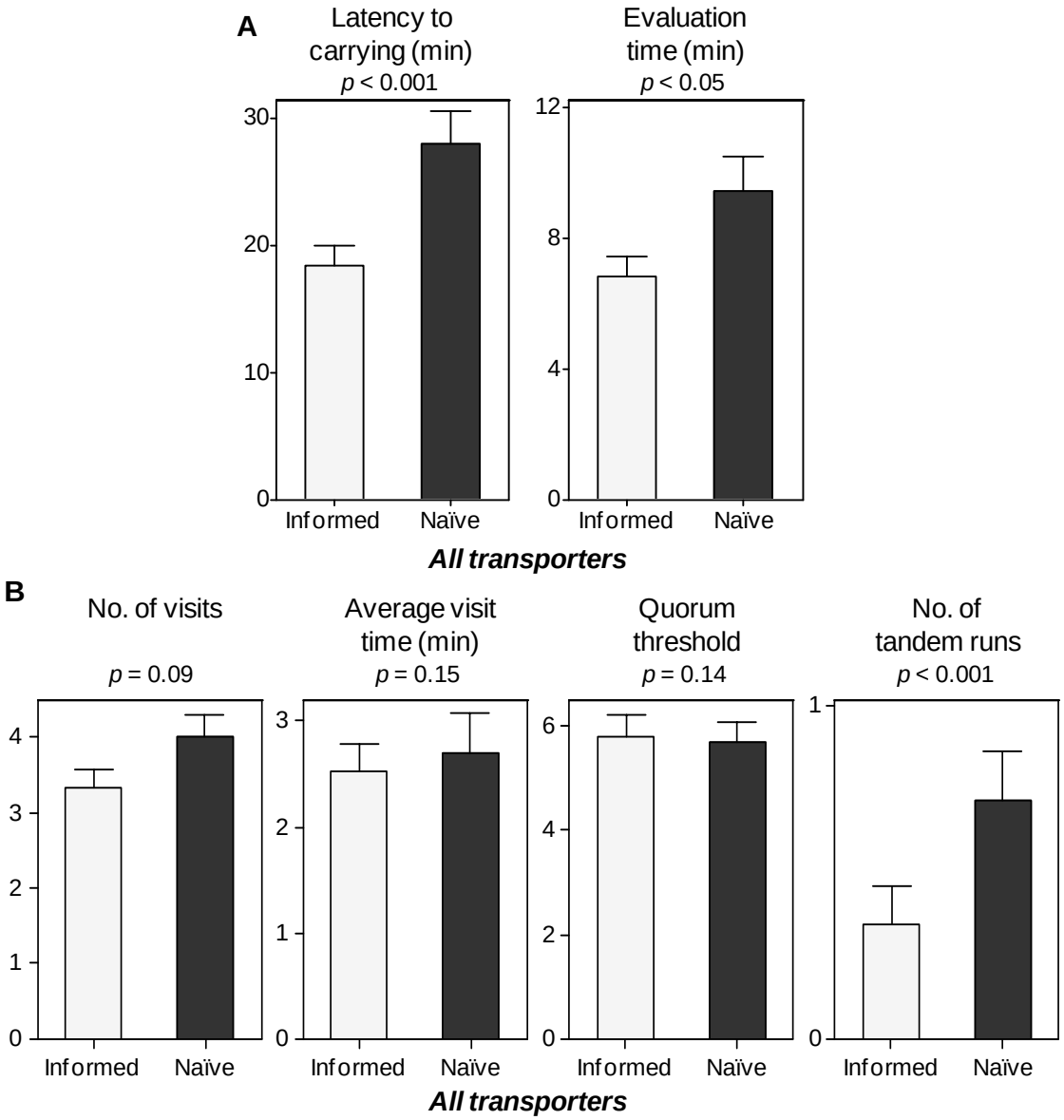

Figure V.14 Transport by all transporters
(A) Latency to first transport and pre-transport evaluation time; **(B)** total number of visits, average visit time, quorum threshold and total number of tandem runs led before the first transport for all individuals involved in transport in informed (light grey) and naïve (dark grey) colonies. Bars and whiskers represent means and standard errors, respectively. *P*-values are given for the effect of treatment on all variables (GLMM; Latency, No. of visits and Quorum threshold were Log-transformed; Evaluation time and Average visit time were power-transformed).

DISCUSSION

In *T. albipennis emigrations*, full commitment to a new nest site follows an assessment period of variable duration, depending e.g. on the quality of the new site (Mallon *et al.* 2001), urgency (Franks *et al.* 2009), or whether the site has been previously visited by exploring workers or not (see Chapter II). In particular, collective decisions are reached earlier for familiar good nest sites than for otherwise identical, unfamiliar nest sites (see p19). The five experiments presented above demonstrate that this results from a complex interplay between private and social information during the evaluation of familiar nest sites.

(1) The role of social interactions

Social interactions between workers inside new sites were *a priori* the most plausible candidate, as full commitment to a site is usually triggered upon the population in that site reaching a quorum threshold (Pratt 2005; Pratt *et al.* 2002). The initial hypothesis was that quorum thresholds are reached earlier in familiar, high-quality nest sites, due to informed workers either being already there or using private information about their location (see Chapter IV). Experimental results indeed showed that the nest population increases faster at familiar than at unfamiliar sites, even when they have been emptied of workers just before emigration (exp. QT1). This faster increase in the population may contribute to expedite decisions about familiar nest sites. Our results however indicate that this alone does not suffice to explain the entire process. Decisions were indeed made at lower apparent quorum thresholds for familiar than for unfamiliar sites (experiment QT1), suggesting that other cues also contribute to the acceptability of familiar sites. Additionally, experimentally induced initial depletion in workers had no effect on the assessment time of familiar sites, but instead resulted in decisions being made at lower apparent quorum threshold values (exp. QT2).

It therefore appears that in addition to altering the dynamics of nest visitation, familiarisation with high-quality nest sites modifies the criteria for nest acceptance. Two alternative interpretations can be advanced: familiarisation could induce either a decrease in quorum threshold (*'lower quorum'* hypothesis), or an increase in independent acceptance probability (*'higher independent acceptance'* hypothesis). These two hypotheses can be formalised mathematically using the following Hill function to model quorum responses:

$$p = a + (m - a)\frac{n^k}{n^k + QT^k},$$

where p is the probability that an individual commits to a nest, a is the probability of independent commitment (i.e. in the absence of social interactions), m is the maximum probability of commitment, n is the number of nestmates already present in the nest, QT is

the quorum threshold, and k is Hill coefficient, a parameter determining the steepness of the quorum response (adapted from Sumpter & Pratt 2009). Figure V.15 shows the shape of typical quorum responses, with parameter values either estimated from experimental results (QT_f and QT_u correspond to the mean quorum threshold values measured for familiar and unfamiliar nests in exp. QT1; a_f and a_u correspond to the proportion of first discoverers independently initiating transport to familiar and unfamiliar nests in the memory experiment), or taken from previous studies on nest assessment by *T. albipennis* (Hill coefficient k was estimated in Pratt 2005; and m was chosen as in Sumpter & Pratt 2009). In the *'lower quorum'* hypothesis, familiarisation induces a decrease in quorum threshold, i.e. $QT_f < QT_u$ (Figure V.15 A). In the *'higher independent acceptance'* hypothesis, familiarisation induces an increase in independent acceptance rate, i.e. $a_f > a_u$ (Figure V.15 B).

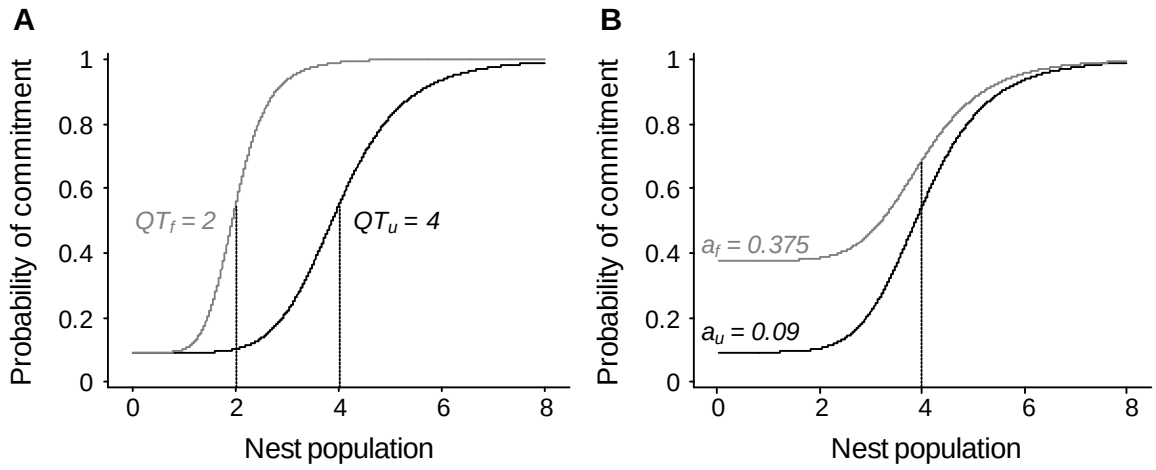

Figure V.15. Quorum responses

Hypothetical quorum responses to identical familiar (f, grey curve) and unfamiliar (u, black curve) good nest sites, assuming that familiarisation with a good nest site lowers the quorum threshold **(A)** or increases the independent assessment probability **(B)**. Unless otherwise stated, parameters are a = 0.09; m = 1; k = 6.3; QT = 4.

The interpretation of approximate quorum threshold values recorded in experiment QT1 should differ fundamentally depending on the scenario. Our experimental design indeed focused only on the first transport decision made in a colony. That first decision could occur during three different phases of the quorum response, namely before, during or after the step-like increase in commitment probability. Given the low value of independent acceptance probability at the unfamiliar site (a_u = 0.09), the first decision is unlikely to occur before the sharp increase in commitment probability. Because the quorum response is steep (with a relatively high Hill coefficient, k = 6.3; see Pratt 2005), this means that the first decision is likely to occur when nest population is relatively close to the real quorum threshold (Figure V.15 A-B). In the *'lower quorum'* scenario, this reasoning also applies to the familiar site (Figure V.15 A), so that experimentally measured quorum threshold values should be as good approximations of the real quorum threshold for familiar as for unfamiliar nest sites. By

contrast, in the *'higher independent acceptance'* scenario, the first decision is more likely to occur before the sharp increase in commitment probability (i.e. when nest population is below the real quorum threshold) in familiar than in unfamiliar sites, because $a_f > a_u$ (Figure V.15 B). In that case, experimentally measured quorum threshold values are more likely to be underestimations of the real quorum threshold for familiar than for unfamiliar sites. In other words, in the *'lower quorum'* hypothesis, quorum sensing still strongly influences decisions for familiar sites, and quorum thresholds are lowered following familiarisation; whereas in the *'higher independent acceptance'* hypothesis, quorum sensing is not the main determinant of decisions for familiar sites, and the low quorum threshold values observed are incidental consequences of expedited decisions.

Further experimental investigations will be necessary to discriminate between these two hypotheses; however, some experimental observations seem to favour the second scenario. In the *'lower quorum'* scenario, we would indeed expect experimental manipulations in exp. QT2 (i.e. initial depletion in workers inside the familiar nest in test colonies) to result in decisions being made at *similar* quorum thresholds in both treatments (since the nest was familiar in both cases), but after *different* assessment times (since the quorum should be reached later in test than in control colonies because of the initial worker depletion). However, opposite trends were observed: decisions were made at *different* quorum thresholds, after *similar* assessment times. This is more consistent with the hypothesis of *'higher independent acceptance'*, suggesting that factors other than social interactions (such as pheromone marking of the nest and/or individual memory, see below) had more influence on the first transport decision than quorum sensing. In that case, the recorded quorum threshold values simply derived from the combination of initial conditions (number of workers inside the nest at emigration start), rate of population increase and duration of the assessment period. Similarly, the observation that first discoverers had a higher chance of immediately initiating transport to familiar rather than to unfamiliar nest sites in the memory experiment strongly supports the hypothesis that familiarisation had induced an increase in independent acceptance probability.

Quorum responses have been argued to be an efficient tool for collective decision-making, partly because they ensure accurate collective choices by delaying individual decisions until a quorum threshold is reached. This allows the collation of information gathered independently by several group members, and reduces the potential impact of individual errors (Franks *et al.* 2002; Pratt *et al.* 2005; Sumpter & Pratt 2009; Visscher 2007; Ward *et al.* 2008). Why do ants forgo this safety mechanism and expedite individual decisions during the assessment of familiar nest sites? The answer may lie in the speed-accuracy trade-off inherent to collective decision-making via quorum sensing. High quorum

threshold values and low independent acceptance probabilities indeed ensure accurate choices and allow the recruitment of enough transporters to ensure speedy emigrations, but at the cost of decision speed (Franks *et al.* 2009; Franks *et al.* 2003a; Marshall *et al.* 2009; Marshall *et al.* 2006; Sumpter & Pratt 2009). For naïve colonies, this may be an advantageous strategy during emigrations, especially if the risk to exposed colonies is low (Franks *et al.* 2003a). By contrast, informed colonies have already invested time and energy gathering and sharing information about the familiar site prior to emigration (see Chapter II), and many individuals already possess private information about that site when emigration starts (see Chapter IV). Maintaining high quorum thresholds and/or low independent acceptance probabilities during emigrations would therefore bring little benefit in terms of choice accuracy and/or total number of transporters. By contrast, the observed strategy of decreasing the influence of social interactions and increasing the relative importance of independent, individual decisions for familiar nest sites (either by decreasing the quorum threshold or by increasing the independent acceptance probability) should result in faster decisions, while maintaining the other aspects of collective performance (see Chapter II). It remains however to be established whether this applies to all workers in the colony (i.e. informed plus naïve), or only to experienced workers.

Social interactions have been shown not to be the sole factor responsible for faster assessment of familiar nest sites; the respective roles of chemical cues and individual memory will now be considered successively.

(2) The role of chemical cues

Experiments P1 and P2 suggest that chemical cues play a role in the assessment of familiar nest sites by both informed and naïve workers. Removing all nest marking chemicals indeed delayed the first occurrence of transport to familiar, high-quality nest sites in both informed and naïve colonies (although that trend was marginally non-significant for informed colonies). Additionally, nest population increased faster (exp. P1) or earlier (exp. P2) during the assessment phase when chemicals were left untouched than when they were removed. At first sight, these results may appear to contradict a previous study on nest assessment by *T. albipennis*, which failed to identify an influence of chemical cues on recruitment behaviour by naïve workers (Pratt 2005). However, that study focused on the nature of the first recruitment decision by naïve individuals and on their latency to initiate the first recruitment act (always a tandem run) after first entering an empty nest that was either unmarked or chemically marked. By contrast, the present study focuses on the overall assessment pattern and may shed new light on the role of chemicals on collective nest evaluation. In agreement with the study by Pratt (2005), we found no differences in the total number of tandem runs led to the new nest site, whether chemical cues had been removed or not. Additionally, first

transport decisions were apparently made at similar quorum threshold values in test and control conditions in both experiments. This suggests that chemical cues did not affect the criteria used for recruitment and commitment decisions. Chemicals appeared instead to operate by influencing the dynamics of nest visitation by workers while evaluating the new nest site and the time necessary to reach these decisions. Repeating both experiments P1 and P2 with individually marked workers and controlled access to the nest (as in the memory experiment) would provide more insight on the effect of chemical cues on individual recruitment behaviour by informed vs. naïve workers, and allow more meaningful comparisons with the previous study by Pratt (2005).

The influence of chemicals previously laid by experienced workers on the evaluation of new nest sites by naïve individuals (exp. P2) shows that information about familiar sites is transferred from informed to naïve workers during the assessment phase. Nest marking chemicals therefore constitute a form of social information about the suitability of a candidate site, potentially used by all individuals. They therefore qualify as pheromones (*sensu* Hölldobler & Wilson 1990). However, it is unclear whether these chemicals are real signals (i.e. specifically aimed at advertising nest site quality), or cues incidentally deposited by workers while exploring the nest. Indeed *T. albipennis* have been shown to leave colony odour cues by simply walking on surfaces (Franks *et al.* 2007a); a nest site impregnated with familiar colony odour might simply be considered more acceptable straightaway by both informed and naïve workers. However, the next section of this chapter (see p117) provides evidence that *T. albipennis* use an aversive pheromone to mark familiar nest sites of low quality; it is therefore conceivable that they might use a corresponding attractive pheromone to mark familiar nest sites of high quality. Further investigations should allow the identification of the pheromones involved and help determine whether they are fortuitous or, on the contrary, whether they represent a specific communication signal.

Interestingly, the influence of pheromones on nest site assessment by naïve workers indicates that the assumption of independent evaluation is violated. According to the theory of the wisdom of crowds, independency is necessary to ensure objective, accurate collective decisions (Janis 1972; Janis 1982; Sumpter & Pratt 2009; Surowiecki 2004). Indeed, we have seen in previous chapters that decisions by emigrating colonies that have previously familiarised themselves with a subset of available nest sites are not always rational or accurate (see Chapter III, p31). For example, colonies presented with a choice between two identical high-quality nest sites showed a clear preference for the familiar over the unfamiliar option (see Chapter II, p21). This would not qualify as an objective decision as defined in previous work on collective decisions, especially in humans. However, as discussed in Chapter III, it may in general be advantageous for ant colonies to exploit previous information

and make biased decisions. This can indeed lead to increased colony performance in terms of emigration speed, group cohesion and occasionally choice accuracy, as shown in Chapter II; additionally, the risk of errors is reduced by compensatory mechanisms acting during the emigration process (see Chapter III) and mistakes can be corrected at relatively low cost through belated improvement emigrations (Dornhaus *et al.* 2004). So, contrary to humans where inter-individual influences can lead to costly 'groupthink' and should be avoided (Janis 1972; Janis 1982; Sumpter & Pratt 2009; Surowiecki 2004), the potential advantages obtained from valuable information transfer from informed to naïve workers in emigrating ant colonies are likely to outweigh the risks of assessment errors induced by non-independent individual evaluation.

Overall, the presence or absence of pheromones inside the new nest had a stronger effect on naïve than on informed colonies. Naïve colonies emigrated significantly faster to chemically marked nests than to unmarked nests, whereas no such difference was observed for informed colonies. This suggests that in informed colonies, the lack of chemical cues was counterbalanced by other sources of information about the familiar site available to informed workers, possibly social interactions and/or individual memory (see below). This illustrates the subtle interplay between different forms of information during the assessment of familiar nest sites. We will now consider more specifically the role of individual memory.

(3) The role of individual memory

The aim of the memory experiment was to investigate whether individual memory by informed workers played a role in evaluation of familiar, high-quality nest sites. All nest marking pheromones were therefore removed at the beginning of emigration by replacing the familiar site by an identical, fresh one, and social interactions were restricted to a minimum by controlling access to the new site. Given the experimental design, the only potential source of information available to first discoverers upon their first entrance in a familiar nest site was their memory, as there were no chemical cues and no other workers present inside the nest. Any differences in the behaviour of first discoverers in test (familiar nest) or in control (unfamiliar nest) conditions can therefore be unquestionably attributed to memory. As the experiment proceeded, new recruits were successively allowed access to the new nest. Chemical communication and social interactions could then take place among workers in the new site. However, because access to the new nest was strictly controlled in exactly the same way for familiar and unfamiliar nest sites, the effect of these interactions should progress over time in a similar way for both treatments. Therefore, to ensure that comparisons were always made at the same stage in the recruitment process, analyses of the behaviour of individual recruiters always included their rank of entrance into the nest as a covariate. Any differences observed between familiar and unfamiliar nest sites can therefore

also be attributed to individual memory with reasonable confidence. Because we did not monitor pre-emigration exploration of the familiar nest, it was not possible to know with certainty whether first discoverers (and their successive recruits) had previously visited the nest, i.e. whether they had had an opportunity to store information about the familiar site in their memory. Overall, first discoverers and recruiters in test conditions (familiar nest) should therefore correspond to a combination of informed and naïve workers, whereas in control conditions (unfamiliar nest), they were all naïve. However, this does not put into question our interpretation of experimental results, as this should result in an attenuation of the effect of memory due to the presence of naïve individuals among analysed individuals in test conditions. Any effect of treatment detected, in spite of this attenuation, would therefore constitute even stronger evidence for the involvement of individual memory.

Analysis of the first recruitment decision by first discoverers provided clear evidence that individual memory of the familiar nest site influences initial individual commitment strength to that nest (equivalent to the independent acceptance probability *a* in the model presented above). First discoverers were indeed more likely immediately to initiate transport to a familiar than to an unfamiliar site. This trend was maintained throughout the observation period, as the same result was obtained when considering all recruiters. Additionally, recruiters were less likely to initiate tandem running and overall individually led fewer tandem runs to the familiar than to the familiar nest site. This confirms that initial individual commitment was stronger, and that less importance was granted to social interactions, as a consequence of informed workers having previously memorised the familiar nest. For workers that did decide to lead tandem runs, however, no differences in behaviour were detected between the two treatments – it could be that these individuals had a low initial commitment to the new site in both test and control conditions, and therefore behaved as if the nest was novel to them. It would be tempting to suggest that tandem leaders in the test might correspond to the faction of naïve individuals recruited to the familiar nest, whereas informed workers did not lead tandem runs – however there is no experimental data to support that claim, and further investigations in which pre-emigration exploration is monitored (as in Chapter IV) are necessary to test this hypothesis.

Individual latencies to first carrying were shorter for familiar than for unfamiliar sites, for both first discoverers and all recruiters. This could be due arguably to informed workers navigating more efficiently from the new nest to the old nest between successive visits to the new site (see Chapter IV, p60) and therefore cannot directly be related to nest evaluation. However, when taking into account only the time spent inside the new nest before initiating transport, this effect remained significant. This indicates that memory of the familiar site induced informed workers to reach a final decision faster than if it was novel; in other words,

less time was required for informed individuals to evaluate the familiar site and deem it suitable. Accordingly, first discoverers initiated transport after fewer visits to the new site, and at lower apparent quorum thresholds, for familiar than for unfamiliar nest sites. This is strong evidence that memory of the familiar site induced a modification of nest acceptance criteria used by informed individuals, e.g. by decreasing their quorum thresholds or by increasing their probability of independent acceptance, as discussed above (sees p108).

As the emigration progressed, the relative influence of memory on individual transport decisions however appeared to decrease. Indeed, when considering all recruiters, there were no differences between treatments in the number of nest visits required before initiating transport, or in the apparent quorum threshold triggering full commitment to the new site. This is probably due to the nest population increasing over time as more and more recruits were allowed access to the nest. As a result, there were more and more opportunities for chemical communication and social interactions to take place, therefore possibly lowering the relative importance of memory. Consequently, the advantages conferred by individual memory might decrease over time, so that naïve individuals using social cues eventually become as likely as informed individuals to commit to the nest. In natural emigrations where there is free access to the nest, one might therefore expect individual memory to play an important role in the beginning of the assessment phase and to influence mostly early transport decisions by a few informed workers. At later stages, memory is likely to be overridden by social cues such as pheromones and social interactions, which may become the main determinants of individual transport decisions by both informed and naïve workers.

In this experiment, individual memories appeared to have an effect on the collective properties of assessment. Overall, collective evaluation of familiar nest sites relative that of unfamiliar nest sites indeed followed similar trends as those presented in Chapter II (see p19). In particular, assessment time was lower, fewer attempted and successful tandem runs were led, and first transport decisions were made at lower apparent quorum thresholds. This indicates that colonies were able to benefit from the information previously gathered by exploring workers about the familiar nest site, even though chemical cues were removed and social interactions restricted to a minimum. Overall, this suggests that individual memories may contribute to enhanced collective performance in emigrations following familiarisation with a suitable nest site.

There are two main hypotheses concerning what specific information is memorised by workers after visiting a high quality, familiar nest: they could memorise the actual quality of the site, or simply memorise that it is suitable – i.e. above a minimum acceptance threshold. In the latter case, informed workers could merely be pre-committed to the new nest site at the beginning of emigration, and the quality of the familiar nest relative to that of

the old nest may influence the proportion of pre-committed workers, as suggested in Chapter III. Further experiments combined with modelling similar to that presented in Chapter III (see p31) and Appendix I (see p159) may help distinguishing between these two alternative interpretations.

General conclusions

In this section, it was shown that both social information (social interactions and chemical communication) and private information (individual memories of informed workers) contribute to the faster assessment of familiar, high-quality nest sites in *T. albipennis*. These different sources of information act in synergy and allow colonies to benefit collectively from the experience of a few informed, key individuals. This is commonly observed in social insects (Anderson & McShea 2001; Anderson & Ratnieks 1999; Fewell 2003; Grüter *et al.* 2008; Leadbeater & Chittka 2007; Leadbeater & Chittka 2009; O'Donnell & Bulova 2007). At this point, it is unclear how social interactions, chemical communication and individual memories interact, and which information dominates. At the individual level, one might predict that memory dominates over social cues, as it is often the case in *Temnothorax* species (see Chapter V, Section A p69, and Aron *et al.* 1988). However, this might not be reflected at the colony level, as the relative importance of private vs. social information may also depend on the proportion of informed vs. naïve workers. Further investigations where an informational conflict between different sources of information is experimentally imposed (as previously done to study navigation, see e.g. Aron *et al.* 1993; Grüter *et al.* 2010; Harrison *et al.* 1989; Hölldobler 1976; Rosengren & Fortelius 1986; Salo & Rosengren 2001) will contribute to a better understanding of the mechanisms of collective assessment of familiar, high-quality nest sites by *T. albipennis* colonies.

After investigating the mechanisms underlying retrieval and sharing of information among workers in emigrations following familiarisation with good nest sites, the next section will aim at investigating the mechanisms underlying aversion to familiar mediocre nest sites.

C – Underlying mechanisms of aversion to low-quality, familiar nest sites

ABSTRACT

The central role of positive feedback in self-organised collective decision-making has long been recognised. Recent empirical and theoretical studies in social insects and ant-inspired computer algorithms suggest that down-regulating processes may also play an important role in collective decision-making, increasing the efficiency and flexibility of decision mechanisms. Here, we report a second example of a 'negative' pheromone in ants, which influences nest site selection by the house-hunting ant *Temnothorax albipennis*. *T. albipennis* gather information about available nest sites prior to emigration, and develop an aversion towards low-quality, familiar nest sites. We show experimentally that colony-level aversion depends critically on the presence of chemicals marking the familiar nest site. Chemical marking of nests is more important in determining colony-level aversion than alternative, position-related cues such as visual landmarks. Finally, we show that nest marking chemicals influence nest assessment by naïve as well as experienced workers, and can therefore be considered as pheromones. Aversive pheromones laid in low-quality familiar nest sites may contribute to effective decision-making in later emigrations, by giving colonies extra time to discover higher quality nest sites, and/or increasing the relative advantage conferred to better sites through recruitment positive feedback.

INTRODUCTION

Information sharing in animal groups is crucial to coordinate the activities of group members. Eusocial insects usually form large societies where communication occurs mostly at a local scale (Camazine *et al.* 2001; Conradt & Roper 2005); however, in certain contexts it may be essential that information possessed by a few well-informed individuals spreads widely through the colony (Fewell 2003; O'Donnell & Bulova 2007). In such situations effective information transfer usually relies mostly on self-organising mechanisms using positive feedback to reach many group members (Camazine *et al.* 2001; Conradt & Roper 2005). Positive feedback mechanisms may also play a central role in collective decision-making, in particular in the context of resource, nest site or path selection by social insects. By amplifying small differences in individual behaviour, positive feedback loops often help the entire group to select collectively the better option (Beckers *et al.* 1993; Bonabeau *et al.* 1997; Camazine *et al.* 2001; Franks *et al.* 2002; Visscher 2007). Although positive feedback mechanisms are sufficient to explain collective choice, recent empirical and theoretical studies have highlighted the role of negative feedback signalling in resource exploitation and path selection, both in real social insects (Robinson *et al.* 2005; Robinson *et al.* 2008; Stickland *et al.* 1999) and ant-inspired problem-solving algorithms (Djamarus & Ku-Mahamud 2008; Ratnieks 2008). For example, the use of 'No entry' repellent pheromone signals at bifurcations by trunk-trail foraging ants such as the Pharaoh's ant *Monomorium pharaonis* (Robinson *et al.* 2005) increases their ability to refocus the foraging effort from exhausted to

new, rewarding food sources, and decreases the risk of being locked on unrewarding trails due to the positive feedback effects of attractive pheromones (Robinson *et al.* 2008; Stickland *et al.* 1999). Negative feedback signals can be expected to play an important modulatory role in many collective contexts (see e.g. Anderson & Ratnieks 1999 for task allocation in honeybees); however, such signals have not been reported so far in nest site selection by house-hunting social insects. In ants, nest choice during emigrations has been shown to depend on quality-dependent amplificatory recruitment processes combined with quorum sensing (Pratt *et al.* 2002; Pratt *et al.* 2005; Richardson *et al.* 2007; Sumpter & Pratt 2009). In other words, the colony's final decision results from the competition between positive feedback loops running independently to candidate nest sites; any modulating process slowing down recruitment in lower-quality nests could thus be expected to amplify any differences in quality between nest sites, and so increase the efficiency of decision-making in way similar to foraging in Pharaoh's ants.

Recent studies on *Temnothorax albipennis* have shown that colonies gather information about available nest sites prior to emigration, and later favour high-quality and avoid low-quality familiar nest sites when they are forced to emigrate (see Franks *et al.* 2007b, Chapter II and Chapter III). As we have seen in previous chapters (Chapter IV; Chapter V, Sections A and B) individual memory, social interactions and pheromone communication all contribute to colonies' collective preference for high quality, familiar sites. By contrast, little is known about the mechanisms underlying aversion towards low-quality, familiar sites, although there is some evidence that it may involve pheromone marking, either outside or inside the familiar nest, as well as visual memory (Franks *et al.* 2007b). In this chapter, we investigate more specifically whether chemical marking inside a familiar, low-quality nest site is necessary for the expression of aversion at the colony level. Additionally, we evaluate the importance of chemical marking of the nest relative to other position-related cues (visual and chemicals) in mediating aversion. Finally, we test whether aversive chemical marking of the nest affects nest assessment by naïve as well as experienced workers. Our results strongly suggest that *T. albipennis* lay chemical marks while visiting low-quality available nest sites, which later act as aversive signals influencing nest assessment by both naïve and experienced workers during emigrations.

METHODS

Two experiments were performed to investigate the relative role of nest marking chemicals and nest position on colony-level aversion. Experiments were performed in large Petri dishes (22 x 22 x 2.2 cm; Figure V.16). Experimental nests had a ceiling height of 1.1 mm and were either bright (mediocre nests) or covered with cardboard to make the interior dark (good nests).

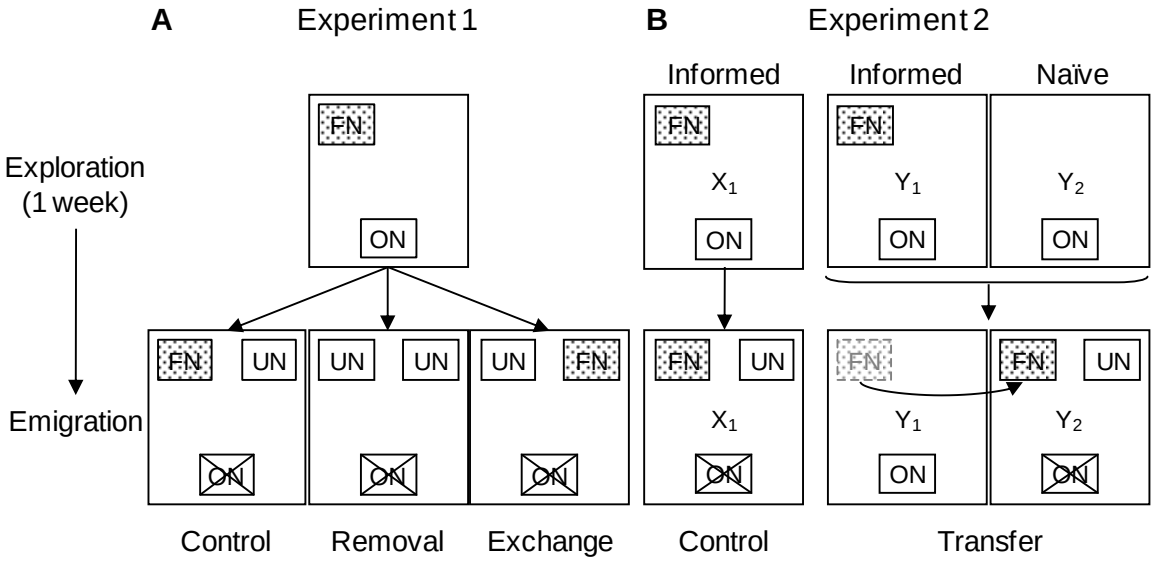

Figure V.16 Experimental designs
Colonies (experiment V.C1) or half-colonies (experiment V.C2) housed in good old nests (ON) were allowed to explore the arena for one week, and then induced to emigrate (crossed nests). During exploration, all colonies in experiment V.C1 and informed half-colonies in experiment V.C2 were allowed to visit a mediocre nest site, whereas naïve half-colonies had no nest site to visit. The position of the familiar nest during exploration (left or right) was pseudo-randomised between trials. During emigration, all colonies had to choose between two identical, equidistant available mediocre nest sites. Available nest sites were either the previously explored familiar nest (FN) or previously unexplored unfamiliar nests (UN). Nest transfers in experiment V.C2 were always done between half-colonies from the same mother colony.

During emigrations, we recorded the discovery time (i.e. the interval between destruction of the old nest and first entrance into the new nest site) of the familiar and unfamiliar nest sites (i.e. nests that, respectively, had and had not been previously explored) for a random sample of colonies in both experiments. Additionally, in experiment V.C2 we counted the number of ants exploring the new nest sites every 5 minutes during the first hour of emigration. For both experiments, the nest chosen by each colony was recorded immediately at the end of emigration and 24 hours after emigration. We evaluated the distribution of the colony 24 hours after emigration as explained in Chapter II (see p18).

Experiments were organised in several blocks (experiment V.C1: three blocks; experiment V.C2: two blocks).

Experiment V.C1 – The roles of positional cues and chemical marking on aversion

Colonies housed in a good nest were allowed to visit a mediocre nest site (familiar nest) during one week, then induced to emigrate (Figure V.16 A). In the control and treatment 'Exchange', emigrating colonies had to choose between the familiar nest and an otherwise identical, but unfamiliar mediocre nest. In the control, the familiar nest was lifted and put back at exactly the same position as during exploration (to control for nest disturbance), whereas in the 'Exchange' treatment, the positions of the familiar and unfamiliar nest sites were switched. A second 'Removal' treatment was also run, in which the familiar nest was removed from the arena and colonies had to choose between two identical, unfamiliar mediocre nest sites.

Twenty-four colonies were tested each under the three conditions 'Control', 'Transfer' and 'Removal' ; the order in which these conditions were experienced was pseudo-randomly varied among colonies.

Experiment V.C2 – Are nest marking chemicals private or social information?

Forty colonies were split into two equal halves (e.g. mother colony Y was split into Y_1 and Y_2). Half-colonies housed in a good nest were allowed to explore the experimental design for one week. During exploration, informed half-colonies could familiarise themselves with a mediocre nest site (familiar nest) whereas naïve half-colonies had no nest site to visit (Figure V.16 B). In the control, informed half-colonies were then induced to emigrate and choose between the familiar and an otherwise identical, unfamiliar nest site. In the treatment ('Transfer'), familiar nests from informed half-colonies were transferred to naïve half-colonies at the end of exploration; naïve half-colonies were then immediately induced to emigrate and choose between the transferred nest and an otherwise identical, unfamiliar mediocre nest site. For the same reasons as presented in the previous section (see p88), transfers were always done between half-colonies from the same mother colony.

Forty colonies were tested each under both control and treatment conditions; 20 colonies were tested first in control conditions whereas the other 20 were tested first in treatment conditions.

Statistical analyses

Nest choice patterns were compared between treatments using two-tailed Fisher-Freeman-Halton's exact tests (Freeman & Halton 1951; Weisstein 2010). Nest preference was tested within treatments using exact binomial tests with a null hypothesis of random choice between both nests (P = 0.5).

Colony distribution was compared among treatments using Friedman tests for three related samples (experiment V.C1, distribution with regard to nest position) or Wilcoxon matched-pairs tests (experiment V.C2 and experiment V.C1, distribution with regard to nest origin, comparison of control and treatment 'Exchange'). Within treatments, colony distribution was compared to random expectations using median tests (P = 0.5).

In both experiments, discovery times of the familiar and unfamiliar nest did not differ across treatments (Mann-Whitney U tests: Experiment V.C1, Control vs. Exchange, familiar site: n = 13, U = 13.0, p = 0.47; unfamiliar site: n = 13, U = 20.0, p = 0.89; Experiment V.C2, Control vs. Transfer, familiar site: n = 27, U = 65.0, p = 0.41; unfamiliar site: n = 27, U = 76.0, p = 0.80) and were therefore pooled for subsequent analyses. Discovery times of familiar and unfamiliar sites were then compared for each experiment using Wilcoxon matched-pairs tests.

In experiment V.C2, the median number of ants inside candidate nest sites during the first hour of emigration was analysed using a covariance analysis with time as a covariate, and treatment (Control or Transfer), nest (Familiar or Unfamiliar) and their interaction as fixed factors. Normality of residuals was checked using a Kolmogorov-Smirnov test (df = 52, KS = 0.074, p > 0.150).

RESULTS

Experiment V.C1 – The roles of positional cues and chemical marking on aversion

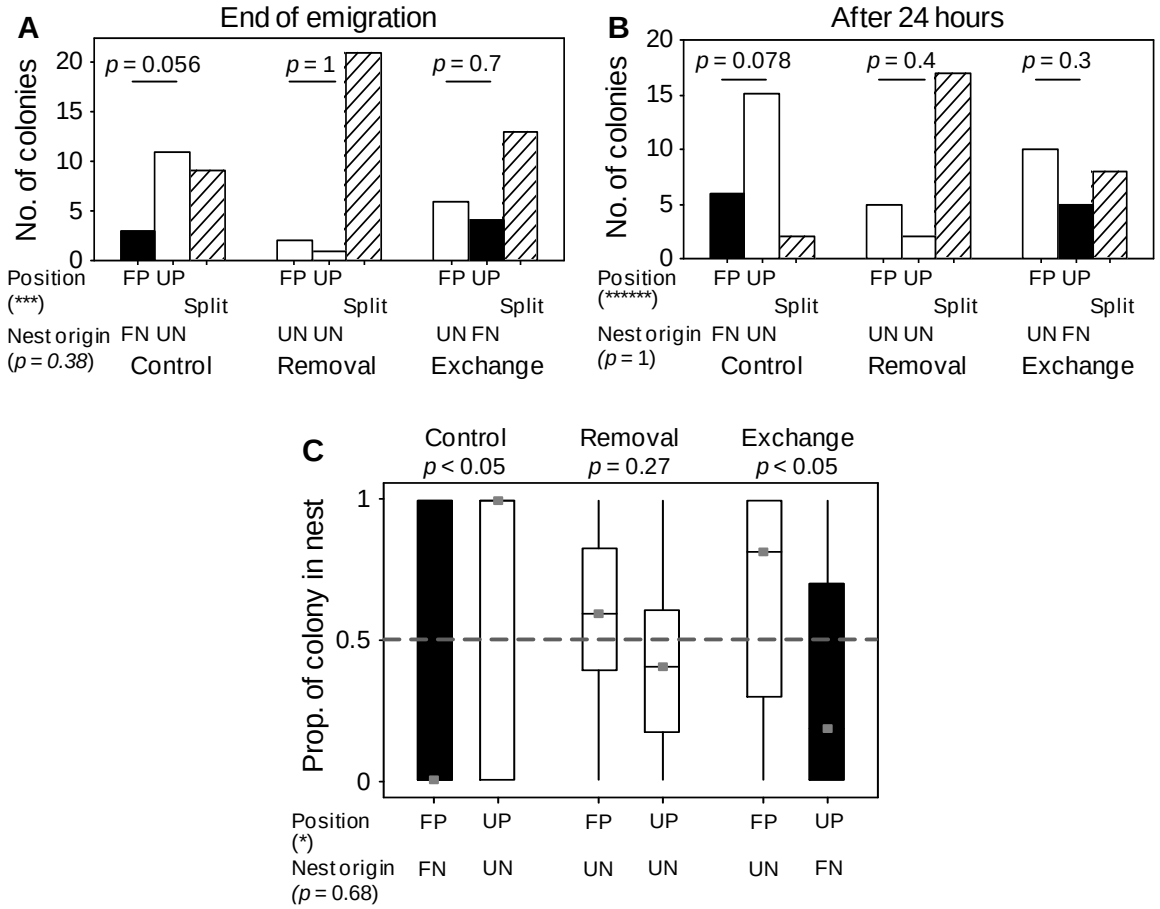

Figure V.17 Nest preference in experiment V.C1
(A-B) Total number of colonies splitting (S; hashed bars) or choosing a nest at the end of emigration **(A)** and 24 hours after emigration **(B)** in experiment V.C1. Nests differed in their position (FP: familiar position, occupied by the familiar nest during exploration; UP: unfamiliar position, on the other side) and in their origin (black bars: previously explored familiar nests, FN; white bars: previously unexplored unfamiliar nests, UN). Nest choice patterns with regard to nest position or origin were compared among treatments using Fisher-Freeman-Halton's exact tests; nest preference within treatments was tested using exact binomial tests. **(C)** Colony distribution 24 hours after emigration (Control: n = 23; Exchange: n = 23; Removal: n = 24). Squares, rectangles, and whiskers respectively represent the median, interquartile range and full range of the proportion of colony items (brood plus adults) observed in each nest. Colony distribution with regard to nest position was compared among treatments using Friedman test for 3 related samples; colony distribution with regard to nest origin was compared among treatments using Wilcoxon matched-pairs test. Within each treatment, distributions were compared to random expectations using median tests with expected median of 0.5.

Nest choice among treatments was not determined by the position of candidate nest sites, either at the end of emigration or 24 hours after emigration (Figure V.17 A-B; Fisher-Freeman-Halton tests: $p < 0.005$ and $p < 0.0001$, respectively). By contrast, nest origin (familiar or unfamiliar) was a good predictor of nest choice, both at the end of emigration and

24 hours after emigration (Figure V.17 A-B; Fisher-Freeman-Halton tests: $p = 0.32$ and $p = 1$, respectively).

When only considering colonies that did not split, we could not detect a significant preference for either nest site (Figure V.17 A-B; binomial tests: $p > 0.05$ in all comparisons). However, analysis of data on colony distribution, including data from split colonies, 24 hours after emigration showed that in both control and treatment 'Exchange', colonies significantly preferred the unfamiliar over the familiar nest (Figure V.17 C; median tests: n = 23, $p < 0.05$ in both treatments). By contrast, in treatment 'Removal', colonies apparently chose randomly between both unfamiliar nest sites (Figure V.17 C; median test: n = 24, $p = 0.27$).

These results indicate that nest choice was not influenced by the position of the nest, but rather by whether it had been previously visited or not. More specifically, colonies apparently developed an aversion towards the familiar, mediocre nest and preferred an otherwise identical, but unfamiliar, mediocre nest.

There was no difference in the discovery time of the familiar and unfamiliar nest sites for the control and treatment 'Exchange' (Figure V.18 A; Wilcoxon matched-pairs test on pooled data: Z = -0.078, n = 12, $p = 0.94$).

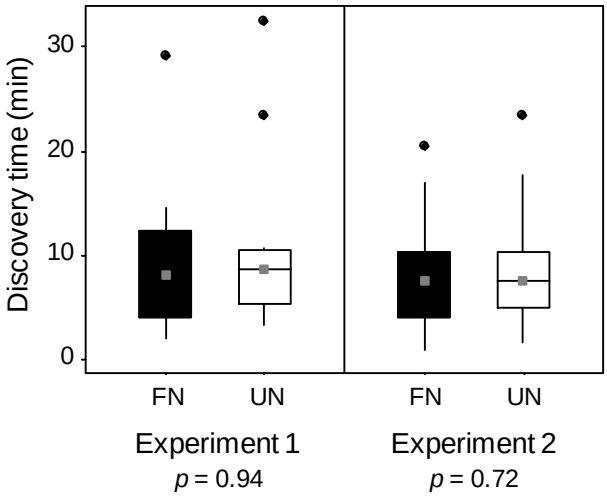

Figure V.18 Discovery times in experiments V.C1 and V.C2
Discovery times of the familiar (FN, black) and unfamiliar (UN, white) nest sites for Experiments 1 (data pooled for the control and treatment 'Exchange'; n = 13) and 2 (data pooled for the control and treatment 'Transfer'; n = 27). Squares, rectangles, whiskers and full circles respectively represent the median, interquartile range, 1.5 x interquartile range and outliers. Discovery times of familiar and unfamiliar sites were compared for each experiment using Wilcoxon matched-pairs tests.

Experiment V.C2 – Are nest marking chemicals private or social information?

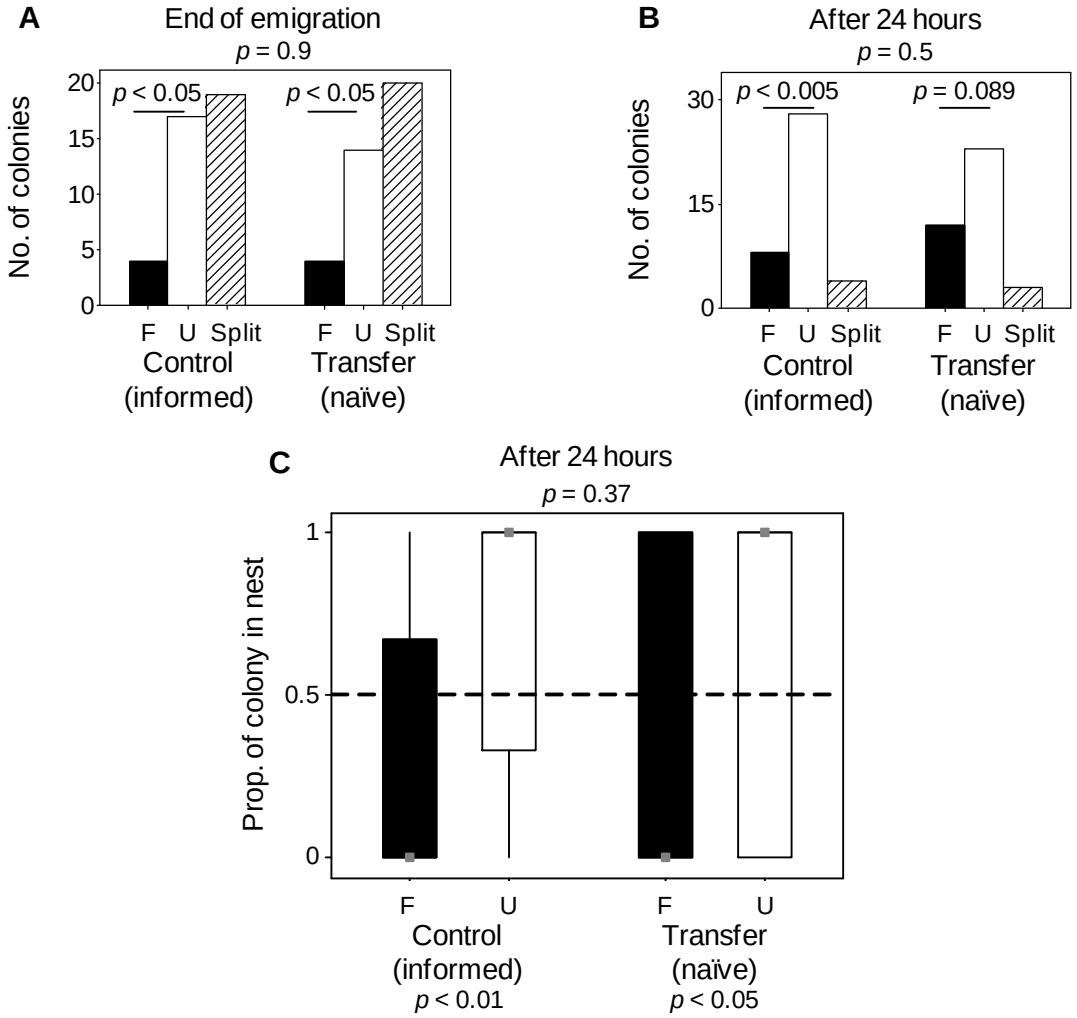

Figure V.19 Nest preference in experiment V.C2
(A-B) Number of colonies splitting (S; hashed bars) or choosing the familiar (black bars) or the unfamiliar (white bars) nest at the end of emigration **(A)** and 24 hours after emigration **(B)** in experiment V.C2. Nest choice patterns were compared among treatments using Fisher-Freeman-Halton's exact tests; nest preference within treatments was tested using exact binomial tests. (**C)** Colony distribution 24 hours after emigration (Control: n = 40; Transfer: n = 38). Squares, rectangles, and whiskers respectively represent the median, interquartile range and full range of the proportion of colony items (brood plus adults) observed in the focal nest. Colony distribution was compared among treatments using Wilcoxon matched-pairs test. Within each treatment, distributions were compared to random expectations using median tests with expected median of 0.5.

Nest choice patterns did not differ for informed and naïve half-colonies, either at the end of emigration or 24 hours after emigration (Figure V.19 A-B; Fisher-Freeman-Halton test: $p = 0.9$ and $p = 0.5$, respectively).

When only considering colonies that did not split, we observed a significant preference for the unfamiliar nest for both treatments at the end of emigration, and for the control 24 hours after emigration (Figure V.19 A-B; binomial tests; end of emigration: $p < 0.05$ in both treatments; 24 hours after emigration, Control: $p < 0.005$; Transfer: $p = 0.089$).

Including data from split colonies 24 hours after emigration showed that in both treatments, colonies significantly preferred the unfamiliar over the familiar nest (Figure V.19 C; median tests; Control: n = 38, $p < 0.01$; Transfer: n = 38, $p < 0.05$).

There was no difference in the discovery times of the familiar and unfamiliar nest sites in both treatments (Figure V.18 B; Wilcoxon matched-pairs test on pooled data: Z = -0.360, n = 27, $p = 0.72$).

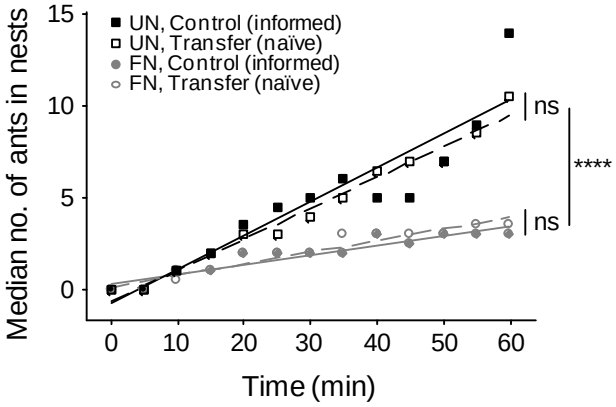

Figure V.20 Evolution in nest population during emigrations in experiment V.C2
Median number of ants in the familiar (FN, grey circles) and unfamiliar nest site (UN, black squares) for informed (Control, full symbols and lines) and naïve (Transfer, empty symbols and broken lines) half-colonies as a function of time during the first hour of emigration in experiment V.C2. Analysis of covariance showed that the median number of ants always increased with time ($F_{1,47} = 120.31$, $p < 0.001$); there was no difference between treatments (ns: $F_{1,47} = 0.06$, $p = 0.81$) and no interaction between nest and treatment ($F_{1,47} = 0.39$, $p = 0.53$), but there was a significant difference between nests (****:$F_{1,47} = 43.76$, $p < 0.001$). The relationships were best described by the following equations: (i) 'Informed', unfamiliar nest: No. of ants = - 0.720 + 0.183 x Time ($r^2 = 0.852$, $F_{1,11} = 63.26$, $p < 0.001$); (ii) 'Naïve', unfamiliar nest: No. of ants = - 0.637 + 0.169 x Time ($r^2 = 0.978$, $F_{1,11} = 481.09$, $p < 0.001$); (iii) 'Informed', familiar nest: No. of ants = 0.319 + 0.0522 x Time ($r^2 = 0.881$, $F_{1,11} = 81.17$, $p < 0.001$); (iv) 'Naïve', familiar nest: No. of ants = 0.143 + 0.0632 x Time ($r^2 = 0.921$, $F_{1,11} = 127.72$, $p < 0.001$).

During the first hour of emigration, scout populations in candidate sites increased with time in a similar way for the control and treatment 'Transfer' (Figure V.20; Covariance analysis; effect of time: $F_{1,47} = 120.31$, $p < 0.001$; effect of treatment: $F_{1,47} = 0.06$, $p = 0.81$; interaction nest x treatment: $F_{1,47} = 0.39$, $p = 0.53$). More specifically, scout populations increased faster in the unfamiliar than in the familiar nest site in both control and treatment (Figure V.20; Covariance analysis, effect of nest: $F_{1,47} = 43.76$, $p < 0.001$).

These results strongly suggest that the familiar nest was marked with chemical cues laid by informed half-colonies which influenced assessment by naïve half-colonies, although they themselves had never been in contact with that nest. These chemical cues resulted in a colony-level aversion towards the familiar nest, as revealed by both emigration dynamics and colony-level choice.

DISCUSSION

T. albipennis colonies can gather information about available nest sites prior to emigration and develop an aversion towards low-quality, familiar nest sites (Franks *et al.* 2007b). We investigated the mechanisms underlying aversion in more detail. Our results show that chemical marking of the mediocre, familiar nest site is necessary to the expression of colony-level aversion, as colonies did not display aversion when chemical marks were removed (treatment 'Removal'). Chemical marking of the familiar nest appeared to be the main determinant of aversion and clearly dominated alternative, position-related cues (e.g. visual cues or chemical marking outside the nest): colonies displayed as strong an aversion towards the familiar nest when the positions of the familiar and unfamiliar mediocre nests where switched (treatment 'Exchange') as in the control. Additionally, naïve colonies were able to decipher the 'message' contained in nest marking chemicals (Anderson & Ratnieks 1999) and showed as strong an aversion to the familiar nest as experienced colonies (experiment V.C2). This indicates that nest marking chemicals were involved in communication between nestmates, and can therefore be referred to as 'pheromones' (Hölldobler & Wilson 1990). Altogether, these results show that colony-level aversion towards low-quality, familiar sites is mainly determined by nest marking aversive pheromones and depends little on individual memories of either the location or the characteristics of the nest. This may seem surprising, as a previous study by Franks *et al.* (2007b) indicated that visual landmarks were also necessary to determine colony-level aversion. However, the experimental manipulations involved in that study were much more disruptive than in the present experiments, and may have mimicked harsh environmental conditions. It has been shown that colonies are much less choosy in harsh conditions and are more likely to split and make mistakes in urgency (Franks *et al.* 2003a). This may explain why the authors were unable to detect any preferences for either the unfamiliar or the familiar mediocre nest after disrupting visual landmarks (Franks *et al.* 2007b).

Overall, the mechanisms underlying storage and retrieval of information about familiar nest sites seem to depend strongly on the quality of these sites. Indeed, although nest marking pheromones contribute to expedite decisions about good familiar nest sites, their role is relatively limited compared to that of social interactions and individual memory (Chapter IV; Chapter V). By contrast, aversive pheromones appear to be the main determinant in deterring colonies from emigrating to previously visited, mediocre sites. The limited role of private information in colony-level aversion also contrasts with previous studies on related *Temnothorax* species, which showed that navigation in familiar areas mainly depends on private information, either via navigational memories or through individual-specific chemical trails (Aron *et al.* 1988; Lane 1977; Maschwitz *et al.* 1986; McLeman *et al.*

2002; Pratt *et al.* 2001). Most interestingly, according to these previous studies, individual-specific chemicals used in orientation in *Temnothorax* sp. cannot be used by naïve individuals (Aron *et al.* 1988; Maschwitz *et al.* 1986), so that recruitment of naïve workers to sites of interest can only occur through direct social interactions such as tandem running (Beckers *et al.* 1989; Möglich 1978). This clearly contrasts with our results showing that naïve workers can respond to aversive pheromones.

The fundamental difference in communication channels used to transfer information to naïve individuals in *Temnothorax* (social interactions vs. aversive pheromones) depending on the context may be due to the nature of the message. Recruitment to good food sources or to good nest sites indeed conveys an essentially positive message, which can easily be amplified through positive feedback. By contrast, information about low-quality nest sites is essentially negative, and cannot be transferred through classical recruitment methods. On the contrary, the presence of informed workers in familiar, mediocre sites would counteract the effects of aversion, as the presence of a worker inside a candidate nest is usually interpreted as a 'vote' in favour of that nest (Franks *et al.* 2002). The use of aversive pheromones allows the circumvention of these constraints and makes it possible for experienced workers to share information about mediocre sites while focussing their own efforts on looking for potential better sites elsewhere during emigrations (Franks *et al.* 2007b).

The use of repellent, negative pheromones has already been reported in social insects: honeybee and bumble bee foragers, for example, mark recently visited flowers with chemicals which repel other foragers until nectar has been replenished (Giurfa & Nunez 1992; Stout *et al.* 1998). A repellent pheromone was also previously described in the Pharaoh's ant, acting as a 'No entry' signal near trail bifurcations which deters workers from entering non-rewarding trails (Robinson *et al.* 2005). This repellent pheromone was shown to increases a colony's ability to focus and reallocate foraging efforts on rewarding trails depending on food availability (Robinson *et al.* 2008; Stickland *et al.* 1999). Our study reports, to our knowledge, the second example of a negative pheromone influencing collective decision-making in ants. Although the mode of action of the pheromone involved in aversion to mediocre nest sites is not known in detail, we believe it is unlikely to act as a repellent 'No entry' signal near the nest entrance, because discovery times were similar for marked and unmarked nests (experiments V.C1 and V.C2). We suggest that rather than triggering an 'on/off' response, the pheromone may act as a modulatory signal (O'Donnell & Bulova 2007), decreasing the probability of nest acceptance by both naïve and experienced workers (Robinson *et al.* submitted; Robinson *et al.* 2009b). This would slow down the recruitment positive feedback loop, resulting in slower population growth, as observed in

experiment V.C2, and therefore delayed commitment to the nest (Pratt 2005; Pratt *et al.* 2002; Pratt *et al.* 2005; Sumpter & Pratt 2009).

Nest site selection by colonies of house-hunting social insects has been suggested to rely on the *wisdom of crowds* (Conradt & Roper 2005; Sumpter & Pratt 2009), whereby groups of individuals are able to make more accurate decisions than isolated individuals (King & Cowlishaw 2007; Krause *et al.* 2010; List 2004; Simons 2004; Sumpter *et al.* 2008b; Surowiecki 2004). Paradoxically, the influence of aversive pheromones on nest assessment by other workers appears to violate a fundamental principle of the *wisdom of crowds*: the independence of assessment by individuals, which is essential to ensure accurate decisions (Sumpter & Pratt 2009; Surowiecki 2004). Indeed, recent work on *T. albipennis* showed that aversion towards familiar, low-quality nest sites can lead to decision mistakes at the colony level in certain conditions. However, in most natural contexts, such aversion is beneficial, as it allows colonies to exploit information about the environment by adjusting their acceptance criteria to local conditions (see Chapter III). We suggest that the use of aversive nest marking pheromones, by delaying commitment to low-quality familiar nests sites, has (at least) two positive effects on nest site selection: (i) it gives colonies more time to discover potential higher-quality nest sites, and (ii) it increases the advantage conferred to higher-quality nest sites by recruitment positive feedback, and therefore the probability of these sites being chosen. Therefore, marking mediocre nest sites with aversive pheromones should improve the effectiveness of nest site selection, provided there are better sites available. Should this not be the case, the quorum threshold would eventually be reached in the familiar nest, allowing colonies to complete their emigration, but with a time cost. *T. albipennis* colonies have been shown to adjust their acceptance criteria to the emergency of the situation, favouring speed in harsh conditions and accuracy in benign conditions (Franks *et al.* 2003a). Because the use of aversive pheromones can incur a time cost to the colony, it may similarly be advantageous for individuals to adjust responsiveness to these pheromones to the emergency of the situation, e.g. by responding less in harsh conditions. Further work may help determine whether this is the case in natural colonies.

We have reported a new example of a negative feedback signal influencing collective decision-making in social insects, and suggested a possible mode of action leading to increased performance in nest site selection by house-hunting ants *T. albipennis*. The advantages conferred by the use of negative feedback signals in collective processes have been reported several times in social insects (repellent pheromones and food exploitation in ants: Robinson *et al.* 2005; Robinson *et al.* 2008; Stickland *et al.* 1999; collisions and path selection under crowded conditions in ants: Dussutour *et al.* 2006; tremble dance and stop signals and foraging task allocation in the honey bee: Anderson & Ratnieks 1999; stop

signals and danger avoidance in the honey bee: Nieh 2010; stop signals and nest site selection in the honey bee: Seeley 2010b) and ant inspired problem solving algorithms (Ant Colony Optimisation, ACO: Ratnieks 2008; Ant System Algorithm: Djamarus & Ku-Mahamud 2008). Many more examples may still be found by studying more closely the mechanisms underlying collective processes in social insects.

GENERAL DISCUSSION

Chapter VI. General Discussion

The general aim of this study was to investigate whether animal groups can exploit, and benefit from, the previous experience and memories of individual group members when making collective decisions. Recent data suggests that this may be the case in groups of vertebrates, especially in the context of navigation. For instance, in homing pigeons navigation in pairs or in larger flocks, some individuals occasionally assume the role of leaders and attract the collective trajectory closer to their familiar route (Biro *et al.* 2006; Nagy *et al.* 2010; Sumpter *et al.* 2008a). In this study, I have shown experimentally that this can also happen in large groups of invertebrates and more specifically in the context of nest site selection during emigrations by rock ants *Temnothorax albipennis*. Rock ant scouts continually explored their environment and stored information about available nest sites. The use of that information in later, forced emigrations allowed colonies to move more efficiently (increased emigration speed, group cohesion and/or choice accuracy; Chapter II). Additionally, familiarisation with available nest sites allowed colonies to make flexible, context-dependent choices, and to adjust their decision strategy to both previously experienced and present conditions (Chapter III). Although this occasionally led to mistakes in nest site selection (Chapter III), the exploitation of previously gathered information was mostly beneficial for emigrating colonies and led to a generally improved collective decision-making performance (Chapter II, Chapter III).

The mechanisms underlying storage, retrieval and sharing of information about familiar nest sites appeared to vary according to the quality of the site. In particular, the relative importance of private vs. social information was strongly contingent on site quality. For example, colonies develop an aversion towards low-quality, familiar nest sites (Franks *et al.* 2007b; Chapter III). Experimental data showed that aversion was principally mediated by pheromone cues, i.e. by social information, and depended little on private, individual experience (Chapter V, Section C). By contrast, the exploitation of information about high-quality, familiar nest sites appeared to rely more strongly on experienced workers that possessed private information about the familiar site (Chapter IV and Chapter V, Sections A and B). Private information was particularly important in the early stages of emigration, during the search for potential new nest sites, as informed workers were able to navigate efficiently towards familiar sites using their memory (Chapter V, Section A). Experienced workers also relied on their memory while evaluating familiar nests (Chapter V, Section B).

However, at that stage information about familiar sites was also transferred to naïve workers through social cues (social interactions and chemical cues, Chapter V, Section B), so that the role of private information relative to social information was less pronounced during assessment (Chapter IV). Evaluation of good familiar nest sites therefore relies on multi-modal sources of information, as is often the case in ants (Hölldobler 1999). The use of multi-modal cues is thought to improve the decision-making abilities of individual foragers in bees (Kulahci *et al.* 2008). In the future, it may be interesting to investigate further the detailed interplay between the different sources of information listed above, and to test whether they also act in synergy to enhance collective decision-making by emigrating ant colonies.

The difference between high and low quality familiar nest sites in the relative importance of private information may be partly due to the mechanisms of decision-making in ant emigrations. The presence of an ant inside a candidate site can indeed be interpreted as a 'vote' in favour of that site (Franks *et al.* 2002; Visscher 2007). The use of pheromones as the main mediator of aversion towards mediocre sites is therefore advantageous, because it allows information to be shared with naïve nestmates without requiring the presence of informed workers – which would partly counteract other aversive effects. By contrast, during emigrations to good familiar nest sites, the use of private information in addition to social cues should bring a supplementary advantage because it contributes to the concentration of the colony's workforce in well-known sites.

Experiments involving split colonies showed that pheromone cues laid by experienced workers influenced nest site assessment by naïve workers, whether the site was good (Chapter V, Section B) or mediocre (Chapter V, Section C). These results are of particularly interest, because they suggest that individuals do not evaluate familiar nest sites independently, in violation of the important criterion of independency underlying the 'wisdom of crowds' (Krause *et al.* 2010; Surowiecki 2004). This may seem surprising at first, as reciprocal influences among group members are believed to amplify individual biases and decrease the accuracy of collective choices in humans (Krause *et al.* 2010; Surowiecki 2004). Similarly, theoretical studies on house-hunting by ants and honeybees have also highlighted the importance of independent initial assessment by individuals to ensure accurate nest site selection (Franks *et al.* 2002; Pratt *et al.* 2002; Pratt *et al.* 2005; Seeley & Visscher 2004a; Sumpter 2006; Visscher 2007).

There are several reasons why ants may resort to non-independent evaluation mechanisms during the assessment of familiar nest sites, even though this is believed to reduce decision accuracy and is strongly advised against in humans (Janis 1972; Sumpter & Pratt 2009; Surowiecki 2004). A first explanation may lie in the constraints on information transfer existing in ants. Contrary to humans, ants lack global communication (Conradt &

Roper 2005) and do not have access to a common pool of knowledge. Instead, information is shared locally among individuals and propagates slowly through the colony via communication networks (Fewell 2003; O'Donnell & Bulova 2007). Additionally, ants do not have a central controller system allowing the examination and comparison of all alternatives before making a final decision (Krause *et al.* 2010). Instead, ants rely on self-organised collective decisions emerging from local individual behaviour (Franks *et al.* 2002; Pratt *et al.* 2005; Visscher 2007). The only effective way to propagate pertinent information possessed by a few key workers (so that collective decisions may benefit from that information) is therefore by inducing appropriate modifications in the behaviour of nestmates, even if this violates the principle of independency. A second explanation is related to the effective costs incurred by non-independent evaluation of familiar nests in ants. Prior exposure to available nest sites did occasionally induce colonies to make mistakes when choosing between two options of different qualities (Chapter III). However, as argued earlier (Chapter V), these errors are very infrequent in most situations (Chapter II, Chapter III), and can be corrected later through reunification and/or a 'move to improve' process (Dornhaus *et al.* 2004). The potential costs of occasionally inaccurate choices are therefore greatly outweighed by the advantages brought by the exploitation of valuable information (Chapter II, Chapter III). Additionally, all colony members share the same interests while searching for a new home (Conradt & Roper 2005). This reduces the risk that some individuals may attempt to bias decision outcomes to serve their own rather than the group's collective interests, as observed in some vertebrate groups where conflicts of interest exist (Conradt & Roper 2009; King & Cowlishaw 2009). Reciprocal influences among nestmates should therefore not be overly detrimental in house-hunting, because natural selection is expected to favour communication mechanisms that increase the entire group's collective performance. Finally, it is interesting to note that the principle of independency is respected in earlier stages of emigration, before assessment: naïve workers are not influenced by informed workers in their search for suitable nest sites (Chapter IV and Chapter V, Section A). Independent exploration allows the discovery of novel, potentially superior alternatives, and ensures that a relatively wide array of options is considered. Such diversity is expected to contribute to improved collective decision-making by increasing the chance of finding the best solution (Surowiecki 2004). To conclude, emigrating *T. albipennis* colonies appear to apply an effective communication strategy maintaining a balance between independency of information gathering in the initial search phase, and propagation of valuable information in the assessment phase. This strategy appears to be very successful, as it leads to improved collective performance in many situations (Chapter II, Chapter III).

The present study raises new questions about house-hunting in *Temnothorax* ants. For example, we observed that high-quality, familiar nest sites are usually occupied by a few

informed workers. An interesting parallel can be made with the green tree ant *Oecophylla smaragdina*, where old workers housed in special barrack nests at the boundaries specialise in guarding and defending the colony's territory (Holldobler 1983). The continual occupation of good available sites by a few workers in *T. albipennis* could similarly correspond to some form of territoriality, and reflect inter-colonial competition over suitable nest sites. It would be interesting to investigate the behaviour of neighbouring colonies in the context of either an excess or a dearth of available sites. Additionally, this study provides new insights with regard to the use of memory in ants. Ants are known to rely on navigational memory to orient in familiar environments (Collett & Graham 2004; Collett *et al.* 2003), and are capable of associative learning in the context of foraging (Dupuy *et al.* 2006; Provecho & Josens 2009). Here, I provided evidence that *T. albipennis* can also 'learn for the future' (as shown in parasitic wasps, see Collett 2008) and memorise information about site quality upon visits of good available nest sites (Chapter V, Section B). However, little is known about the details of the memorisation process, and certain new questions arise. What specific information is stored (i.e., do ants memorise the exact value of the nest, or simply the fact that it is suitable)? How many visits to the site are necessary for memory to be expressed? How long does memory of familiar sites last? When is memory retrieval triggered, and what are the mechanisms involved? Further investigations may help to answer these questions and to understand better the memory process.

Over the last decade, nest site selection by house-hunting social insects have inspired many theoretical models of collective decision-making, focusing on the mechanisms of opinion collation and consensus reaching (Pratt *et al.* 2005; Sumpter & Pratt 2009), inherent speed-accuracy trade-offs (Marshall *et al.* 2006; Planque *et al.* 2007; Planqué *et al.* 2006; Pratt & Sumpter 2006) or the optimality of group decisions (Marshall *et al.* 2009). These models have provided useful insights and testable predictions for the fundamental mechanisms underlying self-organised collective decision-making. However, all theoretical studies have so far assumed that group members are initially naïve. In the previous chapters, I have however provided evidence that in natural conditions, ants gather information about available nest sites prior to emigration, and that this modifies many aspects of the decision process. In particular, the use of prior information has a strong impact on collective preferences (Chapter II, Chapter III), on the relations between emigration speed, group cohesion and decision accuracy (Chapter II) and on the criteria used by workers to fully commit to the new site and initiate transport (Chapter V, Section B). Additionally, the time gap between information gathering and decision-making may also alter optimality criteria (Chapter II). Future models on collective decision making may therefore greatly benefit from taking into account the effects of previous experience. Another assumption common to all theoretical models published so far is that all individuals are identical and have the same

influence on the final decision. However, I have shown that key experienced individuals possessing private information on the location of familiar, high-quality nest sites are particularly influential on the colony's final choice and contribute to these sites being preferred over novel sites (Chapter IV). Future models on collective decision-making and more generally on self-organised processes in large groups could attempt to incorporate such key individuals and investigate how they influence or even shape collective dynamics. Social network approaches, recently applied to the study of division of labour in social insects (Fewell 2003; O'Donnell & Bulova 2007; Sendova-Franks *et al.* 2010), appear particularly well-suited to carry out such investigations.

In general, the results presented in this study confirm that the common juxtaposition of 'individual simplicity vs. collective complexity', although providing a very useful framework for the identification of self-organised, emergent group properties, is an oversimplification. In natural conditions, collective behaviours are likely to be even more complex and to benefit from individual diversity and previous experience. This notion could possibly be applied to engineering domains such as artificial problem solving and Swarm Robotics, e.g. by incorporating previous experience using Bayesian methods (Luttbeg 1996). Interestingly, some research groups have started to study artificial evolution, and in particular the evolution of cooperation, using robots that can autonomously alter their behaviour according to previous experience (Floreano & Keller 2010; Floreano *et al.* 2007; Floreano *et al.* 2008; Mitri *et al.* 2009). The incorporation of experience-dependent behavioural flexibility and inter-individual diversity to Swarm Robotics could possibly open the door to many more fundamental and practical applications.

To conclude, whether future research directions draw inspiration from the present study or not, our results clearly indicate that in ants as in humans, and as Tom Seeley recently claimed about honeybees (Seeley 2010b), individual complexity may greatly contribute to collective complexity.

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APPENDIX

Appendix I. Modelling of Pre-Emigration and Emigration Phases

This appendix details the modelling approach used in Chapter III to investigate whether flexible collective decision-making can emerge from fixed individual decision rules (see p37). The modelling involves two stages, the pre-emigration phase (stage 1) followed by the emigration phase (stage 2).

PRE-EMIGRATION PHASE (STAGE 1)

Pre-emigration commitment behaviour of an independent ant is modelled as a two-state Markov-process, whose state transition matrix is as follows:

$$\begin{pmatrix} h & 1-f \\ 1-h & f \end{pmatrix}, \qquad (1)$$

where the columns (rows) correspond to the states ‘committed to home site’ and ‘committed to familiar site’. Each column gives the probability distribution for that state over the successor states, with *h* being the probability of accepting (or remaining committed to) the home site, and *f* being the probability of accepting (or remaining committed to) the familiar site. Across all experiments, we assume that *h* is larger than *f*. This can occur for several reasons: First, the home site can be of physically greater quality. Second, the home site can be perceived as better due to the presence of brood and the queen. Last, even if old and familiar sites are of the same perceived quality, if we assume a distribution of acceptance thresholds in the colony, then those scouts dissatisfied with the old nest and discovering the familiar site will have a higher average threshold than those scouts staying in the old nest, leading to a correspondingly lower probability of accepting the familiar site. We assume that *h>>f* for experiment III.2, treatment 2, where the home site is of greater physical quality than the familiar site (see p36). We assume that h>f for experiment III.2, treatment 1, where home and familiar sites are of physically the same quality.

Entrance and Exit Events at Familiar Site

We consider that each time a scouts abandons commitment to the home nest and searches for a new one, this generates one entrance and one exit event at the familiar site. For an individual scout committed to the home site the time-steps taken before abandoning commitment is a geometric random variable with mean:

$$\frac{1}{1-h}. \qquad (2)$$

As we assume that *h* in treatment 2 is greater than *h* in treatment 1 (*i.e. h>>f* instead of *h>f*, as described above) it is easy to see that the expected time before abandoning commitment is lower in treatment 1, resulting in more frequent abandonment of commitment to the home site across all scouts and hence increased numbers of entrance and exit events at the familiar site. This pattern is observed in the empirical data (Figure III.6).

Residence in Familiar Site

The limiting probability that a scout is committed to the familiar site at some point in time can be calculated from (1), by application of the Perron-Frobenius theorem, as

$$\mathrm{P}(\text{scout committed to familiar site}) = 1 - \frac{f-1}{f+h-2}. \qquad (3)$$

The qualities of the familiar sites, *f*, are the same in experiment III.2, treatments 1 and 2, but the quality of the home site, *h*, varies. Differentiating (3) with respect to *h* gives

$$\frac{\partial}{\partial h}\mathrm{P}(\text{scout committed to familiar site}) = \frac{f-1}{(f+h-2)^2}, \qquad (4)$$

which is clearly negative (*f* indeed cannot exceed 1 as it is a probability). Thus increasing the quality of the home site, reflected in *h*, decreases the probability that a particular scout is committed to the familiar site at a particular point in time. As commitment to familiar site is associated with a visit to that site, as described above, this therefore predicts that a lower home site quality will result in more scouts on average being in the familiar site at any point in time, in agreement with the experimental data (Figure III.5).

Scouts Committed to Familiar Site at Emigration Onset

Equation (3) also predicts the expected number of scouts committed to the familiar site at the onset of the emigration ('pre-committed ants'), which can be used to set the initial condition for the following model of the emigration dynamics (Figure AI.1).

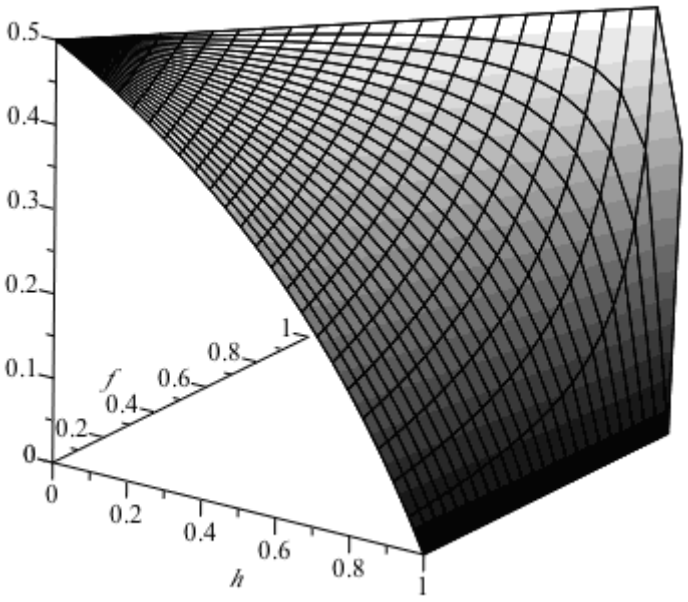

Figure AI.1. Proportion of pre-committed ants as a function of *f* and *h*

EMIGRATION PHASE (STAGE 2)

To model colony-level nest choice by emigrating colonies, we apply an existing stochastic model of opinion formation with recruitment (de la Lama *et al.* 2006; de la Lama *et al.* 2007; Revelli *et al.* 2009). We begin with the microscopic, continuous-time master equation description of the system for the case without any pre-committed ants from de la Lama *et al.* (2006, 2007):

Original model without pre-committed ants

The states in the model are depicted in Figure III.2 B. The total number of ants is N, and the ants are divided into three groups:

- Ants committed to the familiar nest, N_1 ;
- Ants committed to the unfamiliar nest, N_2 ;
- Ants uncommitted to either nest, N_U.

As N is fixed, we have the constraint $N_1 + N_2 + N_U = N$, with only two independent variables N_1 and N_2.

Figure III.2 B also depicts the allowed transitions between states. The corresponding transition rates between these states (which may in general be independent) are as follows:

- Uncommitted ants may spontaneously discover and commit to the familiar nest $U \rightarrow 1$ with rate $\gamma_1 N_U$;
- Uncommitted ants may spontaneously discover and commit to the unfamiliar nest $U \rightarrow 2$ with rate $\gamma_2 N_U$;
- Ants committed to the familiar nest may spontaneously abandon their commitment $1 \rightarrow U$ with rate $\alpha_1 N_1$;
- Ants committed to the unfamiliar nest may spontaneously abandon their commitment $2 \rightarrow U$ with rate $\alpha_2 N_2$;
- Ants committed to the familiar nest may actively recruit uncommitted ants (by tandem running or carrying), which then become committed to the familiar rest $1 + U \rightarrow 1 + 1$ with rate $\rho_1 N_1 N_U / N$;
- Ants committed to the unfamiliar nest may actively recruit uncommitted ants, which then become committed to the unfamiliar rest $2 + U \rightarrow 2 + 2$ with rate $\rho_2 N_2 N_U / N$.

In de la Lama et al. (2006, 2007), the master equation is given for the probability that the system has populations N_1 and N_2 as a function of time. Under the assumption that the parameter $N >> 1$ (which is true for *T. albipennis* colonies, typically of about 100 workers, see Franks *et al.* 2006a), the behaviour of this master equation may then be studied using a van Kampen expansion (see de la Lama *et al.* 2006, 2007 for full details).

The lowest-order term in this expansion results in two coupled differential equations for the mean-field parameters $\Psi_i = N_i/N$:

$$\frac{\mathrm{d}}{\mathrm{d}t}\Psi_1(t) = -\alpha_1 \Psi_1 + \left[\gamma_1 + \rho_1 \Psi_1\right]\left(1 - \Psi_1 - \Psi_2\right)$$
$$\frac{\mathrm{d}}{\mathrm{d}t}\Psi_2(t) = -\alpha_2 \Psi_2 + \left[\gamma_2 + \rho_2 \Psi_2\right]\left(1 - \Psi_1 - \Psi_2\right) \qquad (5)$$

These deterministic equations describe the mean-field, macroscopic behaviour of the system, and have a unique, physically sound attractor (de la Lama *et al.*, 2006). The fluctuations about this mean-field behaviour are determined by the next order in the expansion. These take the form of a bivariate normal distribution determined by the first and second moments of these fluctuations, which are again determined by a set of more involved coupled differential equations (see de la Lama *et al.* 2006, 2007 for full details).

In the steady state, when the system has reached the unique attractor, these sets of coupled simultaneous equations may be solved analytically by symbolic algebra software. However due to their extensive and non-insightful form we do not present them here. From

these we may write down an explicit probability density function $P(\Psi_1, \Psi_2)$ for the variables Ψ_1 and Ψ_2 in the steady state.

Case with pre-committed ants

Following Revelli et al. (Revelli *et al.* 2009), the above model may be extended to incorporate an initial proportion ϕ of ants already committed to the familiar site at the onset of emigration. We consider these 'pre-committed ants' to remain committed to the familiar nest during the entire decision making process; they may not spontaneously abandon their commitment to the familiar nest, but crucially may recruit uncommitted ants, which then become to become committed to it in the normal way. In the mean-field, we denote the ants committed to the nests in the normal way as ψ_i, such that $\Psi_1 = \psi_1 + \phi$ and $\Psi_2 = \psi_2$. The resulting mean-field equations are as follows:

$$\frac{\mathrm{d}}{\mathrm{d}t}\psi_1(t) = -\alpha_1\,\psi_1 + \left[\gamma_1 + \rho_1\,(\psi_1 + \phi)\right](1 - \psi_1 - \psi_2 - \phi)$$
$$\frac{\mathrm{d}}{\mathrm{d}t}\psi_2(t) = -\alpha_2\,\psi_2 + \left[\gamma_2 + \rho_2\,\psi_2\right](1 - \psi_1 - \psi_2 - \phi) \qquad (6)$$

These equations may again be solved explicitly in the steady state. As the fluctuations in the model are determined by the next order in the expansion of the master equation and that ϕ is small, we assume to a first approximation that they remain unchanged from above. We may therefore again immediately write down an explicit probability density function $P(\Psi_1, \Psi_2, \phi)$ for the variables Ψ_1 and Ψ_2 in the steady state, this time also as a function of the proportion of pre-committed ants ϕ.

Parameter assumptions

As the perceived quality of a nest decreases, we assume that the rate at which ants spontaneously commit to it also decreases, whilst at the same time the rate at which they abandon it increases. We model this relationship as being inversely proportional, such that $\alpha_1 = 1/\gamma_1$ and $\alpha_2 = 1/\gamma_2$. Furthermore, as it is harder to find a nest than it is to leave it, we assume that for a given nest, the rate of spontaneous abandonment is greater than the rate of spontaneous commitment, such that $\alpha_1 > \gamma_1$ and $\alpha_2 > \gamma_2$.

As ants have been shown to recruit more readily to higher quality nest sites (see e.g. Mallon *et al.* 2001; Robinson *et al.* 2009b), we further assume that the rate at which committed ants actively recruit uncommitted ants increases linearly with increasing nest quality, such that $\rho_1 = \gamma_1$ and $\rho_2 = \gamma_2$. Changing the constant of proportionality by an order of

magnitude in either direction in this assumption does not qualitatively change results and conclusions of the model, as illustrated in Figure AI.2.

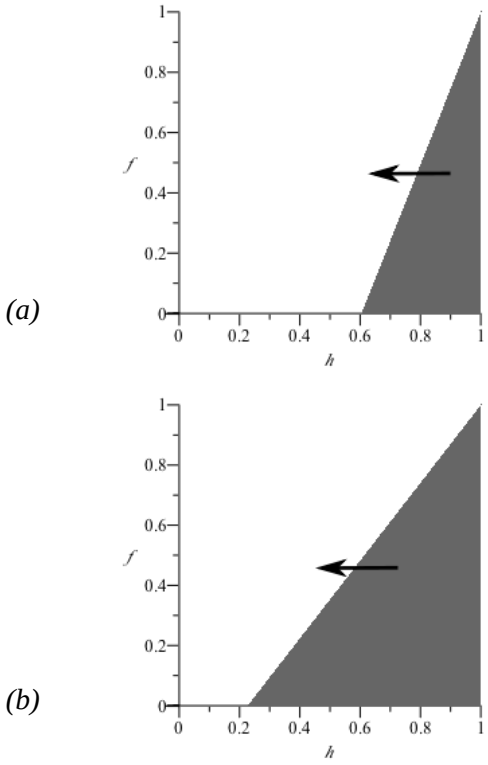

Figure AI.2

Predictions from combined pre-emigration and emigration phases for colony-level nest choice for cases in which *(a)* $\rho_i = 0.1\ \gamma_i$ and *(b)*$\rho_i = 10\ \gamma_i$. The shaded region indicates the values of *h* and *f* in the pre-emigration model in which the unfamiliar site is more likely to be chosen. In the unshaded region the familiar site is more likely to be chosen. Along the line dividing the regions the colony choice will be random (see below). The results and conclusions do not qualitatively differ from the case presented in the main text (Figure III.7) where it is assumed $\rho_i = \gamma_i$.

With these assumptions we have reduced the number of free parameters in the model from seven to three: α_1, the rate of spontaneous abandonment of the familiar nest (which can be considered a measure the 'poorness' of the familiar nest); α_2, the rate of spontaneous abandonment of the unfamiliar nest (which can be considered a measure the 'poorness' of the unfamiliar nest); and ϕ, the proportion of pre-committed ants.

Analysis

We wish to now calculate which nest is more likely to be chosen by the colony as a function of the quality of the original home nest relative to the quality of the familiar nest. We model that the colony chooses the nest to which the majority of ants have committed themselves (which we assume occurs once the system has reached its steady state). This may be found by integrating the probability density function $P(\Psi_1, \Psi_2, \phi, \alpha_1, \alpha_2)$ either side of the line $\Psi_1 = \Psi_2$. If the integral bounded by the Ψ_1-axis is greater, it is more likely that the

majority of ants will be committed to the familiar nest 1, and so this nest is more likely to be chosen. Conversely, if the integral bounded by the Ψ_2-axis is greater, it is more likely that majority of ants will be committed to the unfamiliar nest 2, and so this nest is more likely to be chosen.

However, due to the Gaussian symmetry of $P(\Psi_1, \Psi_2, \phi, \alpha_1, \alpha_2)$ about the mean-field solution, we know that the integral bounded by the Ψ_1-axis will always be greater if the mean-field solution is in the region, and similarly for the integral bounded by the Ψ_2-axis. Hence in order to find which nest site is more likely to be chosen by the colony for particular parameters ϕ, α_1 and α_2, we simply need to calculate which side of the line $\Psi_1 = \Psi_2$ the corresponding stationary mean-field solutions Ψ_1^{st} and Ψ_2^{st} (which are functions of these parameters) lie.

The surface $\Psi_1^{st}(\phi, \alpha_1, \alpha_2) = \Psi_2^{st}(\phi, \alpha_1, \alpha_2)$ therefore defines a boundary between the two distinct regions in the $\phi - \alpha_1 - \alpha_2$ space in which one nest is more likely to be chosen over the other. This surface is depicted in Figure AI.3, which shows the proportion of pre-committed ants required for random nest choice as a function of α_1 and α_2 under the above assumptions. As can be seen, this required proportion is usually quite small, with a maximum possible value of approximately 30%.

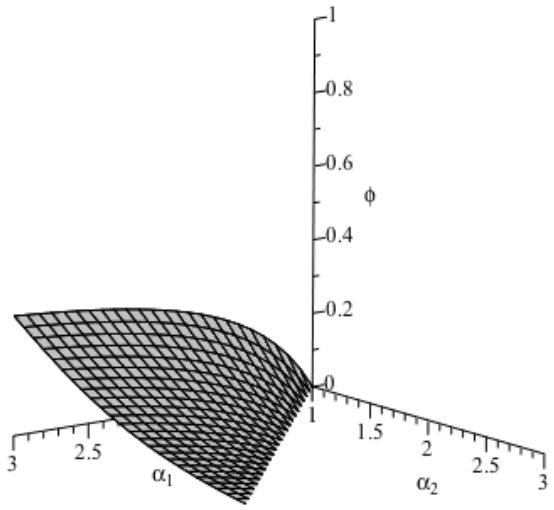

Figure AI.3
Surface $\Psi_1^{st}(\phi, \alpha_1, \alpha_2) = \Psi_2^{st}(\phi, \alpha_1, \alpha_2)$ showing the proportion ϕ of pre-committed ants required for random colony choice as a function of α_1 and α_2.

This figure also shows that random nest choice cannot occur for non-negative values of ϕ if the abandonment rate for the familiar nest is lower than for the unfamiliar nest (i.e. $\alpha_1 < \alpha_2$). In other words, random nest choice can only occur if the perceived quality of the unfamiliar nest is higher than that of the familiar nest. This is consistent with the biological context studied here, where colonies overall develop an aversion towards the familiar nest site so that its overall perceived quality is lower than that of the unfamiliar site, presumably resulting in lower commitment rates ($\gamma_1 < \gamma_2$) and higher abandonment rates ($\alpha_1 > \alpha_2$). In this context, random colony choice as observed in experiment III.2, treatment 1 can occur if a small proportion ϕ of scouts with low acceptance thresholds are pre-committed to the familiar nest, counteracting the effects of overall aversion (see main text for details). Conversely, if the perceived quality of the familiar nest is higher than that of the unfamiliar nest, the presence of pre-committed ants can only reinforce the effect of nest quality, so that random nest choice cannot occur – as confirmed by the model.

For fixed α_2, the general shape of the resulting curve in the corresponding $\phi - \alpha_1$ plane does not qualitatively change. Hence we may fix α_2, the 'poorness' of the unfamiliar nest (we choose as a reference a low number α_2 = 5/4 distinct from unity to avoid any potential pathological behaviour). This reduces the number of free parameters in the model to just two: α_1 and ϕ.

However, the results of the pre-emigration model give an expression for the expected number of ants committed to the familiar site at the onset of the emigration (Equation (3)), which we equate to the ϕ of this model:

$$\phi = 1 - \frac{1-f}{2-f-h} \qquad (7)$$

This allows us to calculate which nest is more likely to be chosen by the colony as a function of the quality of the original home nest (*h*) relative to the quality of the familiar nest (*f*).

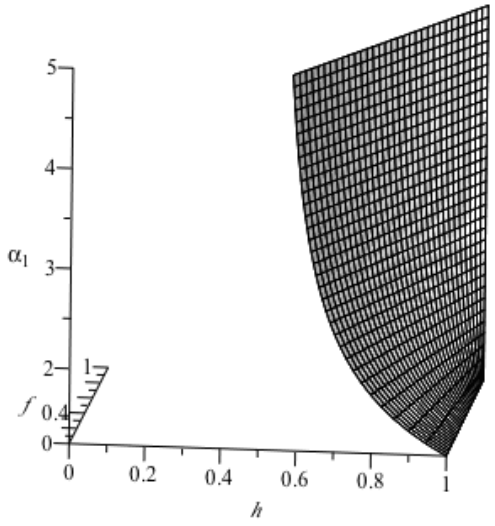

Figure AI.4
Surface $\Psi_1^{st}(\phi, \alpha_1) = \Psi_2^{st}(\phi, \alpha_1)$ showing the values of *h*, *f* and α_1 for which nest choice is random.

The relationship $\Psi_1^{st}(\phi, \alpha_1) = \Psi_2^{st}(\phi, \alpha_1)$ defining the boundary between the two distinct regions in which the different nests are likely to be chosen is now the surface in *h*–*f*–α_1 space depicted in Figure AI.4.

If the stationary mean-field solution lies above the surface in Figure AI.4, the unfamiliar site is more likely to be chosen; below the surface the familiar site is more likely to be chosen. Except in the region of small α_1 and small *f*, this surface is almost a flat plane independent of α_1. We argue that for biologically realistic parameters it can be approximate as such. The parameters *f* and α_1 are indeed both a measure of the quality of the familiar nest, used in two different models. However *f* is a measure of the 'goodness' of the familiar nest, whereas α_1 is a measure of the 'poorness' of the very same nest. It is therefore biologically unrealistic for both values to be simultaneously low, as – whilst not necessarily inverses of each other – these two parameters are negatively correlated.

Hence, to a very good approximation, the surface shown in Figure AI.4 can be approximated to a flat plane independent of α_1. The projection of this plane onto the *f*-*h* surface is presented in Figure III.7.